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SAMUEL N. SPRING, Dean

Technical Publication No. 59

THE RELATION OF CERTAIN METEOROLOGICAL FACTORS TO THE INFECTION OF EASTERN WHITE PINE BY THE BLISTER-RUST FUNGUS

BY

RAY R. HIRT, Ph.D.

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THE RELATION OF CERTAIN METEOROLOGICAL FACTORS TO THE INFECTION OF EASTERN WHITE PINE BY THE BLISTER-RUST FUNGUS

By RAY R. HIRT[1]

INTRODUCTION

The blister-rust disease of eastern white pine, *Pinus strobus* L., is caused by the fungus *Cronartium ribicola* Fisch. This pathogen requires 2 different kinds of hosts, ribes and 5-needled pines, for the completion of its life cycle. It becomes established upon its pine hosts only by means of spores, known as basidiospores or sporidia, that are produced on ribes leaves and transmitted to pine needles chiefly by the wind. The production and germination of the sporidia are dependent in part upon favorable weather, particularly suitable temperatures and the presence of free water. Thus, when rust-infected ribes are present, the natural infection of eastern white pine is determined largely by certain favorable meteorological factors.

Weather conditions may vary appreciably between neighboring localities; they vary also from day to day and from year to year. Consequently, within the range of eastern white pine, there are some areas as well as some seasons that are more or less favorable, or unfavorable, for the intensification of the blister-rust fungus. Information regarding the influence of different weather conditions upon the infection of eastern white pine may find application in the problem of control as exercised through silvicultural and management practices. To be most effective, the program for the control of this disease must take into account the effect of weather during a season that is extremely favorable for the spread of the blister-rust fungus. Such a program must recognize also that, in order to obtain effective control, pine stands in certain localities where ribes are abundant and where favorable temperature and moisture conditions prevail year after year may need unusually intensive and extensive ribes eradication. On certain localized sites where effective ribes eradication is difficult and where the prevailing weather between late spring and autumn is especially congenial to pine infection year after year, it may even be wise to avoid planting *P. strobus*.

It is not feasible, within the limits of a single investigation, to obtain a complete understanding of the many phases and interrelationships of the fungus, the hosts, and the meteorological environ-

[1] This study was made by the writer while employed as agent in the Bureau of Plant Industry, United States Department of Agriculture, in cooperation with the New York State College of Forestry, Syracuse, New York.

ment; hence this study is concerned with only a few of the influential environmental factors acting within a limited range of the pathogen and of eastern white pine. It is possible that some of the results of the study may have general application to the control of the fungus in other regions and on susceptible 5-needled pines other than *P. strobus*.

MATERIALS AND METHODS

When investigating a plant disease it is usually desirable to conduct the studies under natural conditions, but in order to understand better the effects of individual factors, it is sometimes necessary to make additional studies under controlled conditions, which may create artificial or semi-artificial environments for the organisms concerned. Both artificial and natural environments were employed in this investigation.

The studies were begun in 1927 by Dr. L. H. Pennington (15) who directed the work until his death in 1929, when the writer took charge. The field and laboratory work has been conducted in a similar manner each summer from 1927 through 1938, although some modifications were made in the method of study from time to time as experience suggested. The studies were made near Warrensburg, New York, from 1927 to 1933 inclusive and near Syracuse, New York, from 1934 to 1938 inclusive. The trees that were used in 1934 were burned accidentally the following year; therefore, throughout this paper no data for that year are included except in 1 instance where it is so stated. From 1927 to 1929 inclusive, the work consisted largely of experimentation in the methods of making and recording observations, so that prior to 1930 very little conclusive data were secured.

The procedure from year to year was approximately as follows: In April, healthy trees of 2–1 and 2–2 planting stock of eastern white pine were potted in top soil in 6-inch or 8-inch Neponset paper pots. The potted pines were set in soil to a depth of approximately 6 inches in storage beds where they remained until needed for experimental purposes. The pots remained sufficiently firm so that, when handled later, the root systems of the trees were undisturbed (Fig. 1). The storage and planting areas of the pines were protected from blister-rust infection according to methods recommended by the United States Department of Agriculture (11).

A garden of cultivated European black currant, *Ribes nigrum* L., was established at a safe distance, under the local conditions, from the storage and planting areas. In the Warrensburg experimental area ribes were infected by naturally disseminated aeciospores of *C. ribicola;* in the Syracuse area, ribes infection resulted from dusting the ribes leaves with freshly produced aeciospores secured from infected pines near Warrensburg, New York, during April or early May. The gardens were located in the open and subject to direct sunlight so that many of the infected ribes leaves either died or became

hardened by midsummer, and teliospore production almost ceased. In order to insure a constant supply of viable teliospores in the gardens throughout the summer and autumn, an additional supply of infected bushes of *Ribes nigrum* were grown in individual tubs of soil placed in a moist location in a nearby forest. These partially shaded bushes retained most of their infected leaves in a nonhardened condition so that some of the bushes had viable teliospores throughout the summer. These potted bushes were introduced into the garden

Fig. 1. Young pines were set in Neponset paper pots, which enabled them to be handled without disturbing the root system.

as needed in order to supplement the failing supply of telia on the permanently planted bushes. In late August the latter bushes usually formed new leaves that became infected and in turn produced telia. By keeping viable teliospores constantly in the garden, it was possible each season to study the relation of the daily meteorological conditions to pine infection.

Weather records in the garden and planting areas were secured by use of a standard rain gauge, a hygrothermograph, a sun recorder, a barometer, and an instrument for recording the duration of rainfall

(6). General observations and records were made of wind direction and velocity, periods of dew and fog were recorded, and pertinent notes were made relevant to the condition and development of the fungus and the pines. In each of the experimental areas a damp chamber was used for certain purposes as subsequently explained. Each chamber was constructed of wood, covered with burlap, and placed on supports slightly above the water level of a small stream flowing from a spring. Water was piped from the spring so as to flow over the roof of the chamber and keep the burlap wet. The damp chamber at Warrensburg maintained a relative humidity of 96 to 100 per cent and a temperature almost constantly between 50°F. and 60°F. (Fig. 2, B). The damp chamber near Syracuse had a tem-

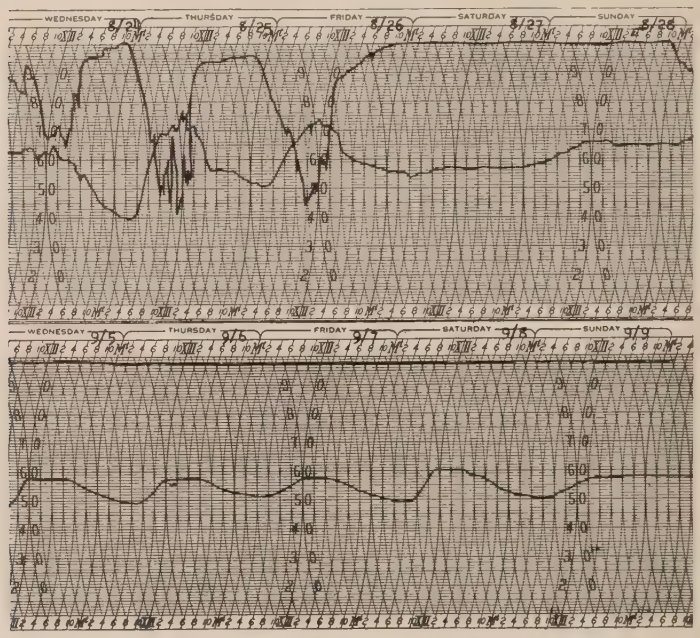


Fig. 2. A. The record of relative humidity and temperature for August 26 and 27, 1927, when pine infection occurred. B. A 5-day record of the relative humidity and temperature in the damp chamber at Warrensburg, New York.

perature that ranged mostly between 57°F. and 68°F. and kept a relative humidity of approximately 100 per cent. These damp chambers were used solely to determine the presence of sporidia in the ribes garden as explained subsequently.

Each season, as soon as telia developed upon the leaves of the ribes

in the garden, the actual experimental work was begun. For the purposes of the study, each 24 hours was divided into two 12-hour periods corresponding roughly to daylight and darkness, 8 A.M. to 8 P.M. and 8 P.M. to 8 A.M. Twelve or 15[2] potted pines were taken from the storage beds at the beginning of each 12-hour period and placed on the ground in the garden close beside the infected ribes bushes (Fig. 3). They were left in that position for 12 hours and then replaced by another set of 12 or 15 potted pines. At the end of each 12 hours, 2 or 5 of the exposed pines, depending upon the year of the test, were placed in a damp chamber for 36 hours and then planted in a permanent planting area. Hereafter these particular pines will be referred to as damp-chamber plants. Five or 10 of the exposed pines were taken directly from the ribes garden to the planting area where they were placed in the ground without removing the paper pots. Within the plantations thus established,

Fig. 3. A section of the ribes garden, showing how potted pines were exposed to telium-bearing bushes of *Ribes nigrum*. The potted ribes bush was used to supplement the supply of telia on the leaves of the non-potted ribes, which became almost defoliated in midsummer.

the pines were arranged in rows and in certain positions within each row, so that the position of a tree served as a key to all the recorded information regarding its history in the experimental work. The blister-rust cankers that developed on these pines were from needle infections that resulted from sporidia falling on the needles while the

[2] The difference in the number of potted pines that were used was the result of minor changes in the work.

pines were in the ribes garden,[3] during a period when the prevailing meteorological conditions were known. Each month, except from December to February or March inclusive, the trees were examined for mortality, state of health, presence of cankers, condition of cankers, and other pertinent data.

During several years, from 85 to 100 pines, hereafter designated as season-exposure pines, were planted close beside the ribes bushes and thus were continuously exposed to rust infection throughout an entire season. Comparisons were made between the development of blister-rust cankers on natural reproduction in the nearby forest and on potted pines in order to detect differences that might occur in the development of the rust under strictly natural conditions and under the conditions of the experiment. Except in the degree of infection no differences were observed. During some years, species of 5-needled pines other than *Pinus strobus* were also used (8).

RESULTS

SPORIDIUM PRODUCTION

The penetration of pine needles by the germ tubes from sporidia of *C. ribicola* (2, 7) is preliminary to the formation of bark cankers in *P. strobus*. Sporidia are formed subsequent to the germination of teliospores that compose the telial columns that develop on the under side of infected ribes leaves (3, 10, 17, 18). Therefore, one of the requisites for pine infection is favorable weather for teliospore germination. Studies have been made under both natural and controlled conditions concerning the relation of moisture, temperature, sunlight, drying, and other factors to the production and germination of sporidia (5, 18, 22).

Time of production.—In the vicinity of Warrensburg, New York, telia were observed first on naturally infected *Ribes nigrum*, *R. rotundifolium* Michx., and *R. prostratum* L'Hérit. on the following dates: 1929, July 10; 1930, July 25; 1931, June 16; 1932, June 30; and 1933, June 21. The exact conditions that determine the time of production of telia and sporidia from year to year are unknown, but probably these conditions are largely the meteorological variations from season to season, which influence the time of aeciospore production and the development of ribes leaves. The writer observed that telia were formed on ribes more or less simultaneously throughout widespread areas in the Adirondacks of New York State[4] and it is possible that this may hold true for more extensive areas. Teliospores were produced in pronounced waves or crops 2 or more times during

[3] Less than one-half of 1 per cent of the trees became infected from outside sources from 1927 to 1937 inclusive.

[4] This has been confirmed verbally for ribes in the Adirondacks by Mr. A. E. Fivaz, formerly of the Division of Blister Rust Control, and by Dr. W. H. Snell, Brown University, Providence, Rhode Island.

a growing season. The crops of teliospores were apparently associated with renewed leaf formation as well as with seasonal weather changes. Under the conditions of the experiments, *R. nigrum* became almost defoliated during August and then produced a new set of leaves. The young leaves became infected from urediospores produced in the older leaves and the rust developed as it did in the young leaves formed in the spring. The formation of telia took place when the leaves were mature or nearly so. During extended periods of clear, hot days in midsummer, the mature infected leaves that remained on the bushes and that were exposed to the sun changed in color to a dark shade of green and then became somewhat tough and hard in texture. On these hardened leaves, teliospore development almost ceased. The leaves of the potted ribes that were not exposed to direct sunlight and that were kept under cover of the forest remained light green and flexible, and a few telial columns continued to develop even between the pronounced waves of telium production.

In the autumn, while urediospores were forming upon the newly infected young leaves produced in the late summer, urediospores also developed once again upon the few old, infected, hardened leaves that had persisted throughout the season. New telial columns were then produced upon the leaves formed in both spring and autumn. Apparently certain seasonal factors as well as leaf maturity and condition acted as a stimulus for teliospore production.

Teliospores become mature soon after they are formed. Therefore the tip cells of a telial column may produce sporidia while the column is still elongating due to the production of young teliospores at the base. Telial columns only 24 hours old were found with their tip cells producing sporidia when weather factors favored their development (5). The prevailing moisture conditions and temperatures were propitious for teliospore germination almost every night in the experimental areas, particularly at Warrensburg; consequently, most of the telial columns 24 hours old and older had a few newly germinated teliospores every day. This gradually reduced the number of viable teliospores in the telial columns and also made a few sporidia available each night for the infection of white pine. Usually the sporidia produced under these night conditions were so few and were formed so late in the night that the possibility was very slight for them to contact pine needles and establish infection prior to the inhibiting effects of the dry, warm air of most of the daylight periods. In this nightly process of sporidium production, many basidia were formed too late to reach the stage of sporidium production by morning; some of these immature basidia were able to survive the heat and low relative humidities of days with sunshine, and the following night to renew their development and eventually to produce sporidia. These partly matured basidia were found to produce viable sporidia within 3.5 hours after favorable meteorological conditions occurred. Mature, ungerminated teliospores required

approximately 11 to 12 hours for sporidium production. This nightly process of sporidium production must have appreciably reduced the potential danger to near-by pines, which would have existed during extended periods of favorable infection weather if all of the telial columns had been composed only of ungerminated teliospores.

Sporidium production started on variously aged telial columns at approximately the same time after suitable weather conditions occurred, but maximum production was reached within the shortest average time by columns that ranged in age between 96 and 216 hours. The reason for this seemed to be that most of the teliospores in a telial column were mature at 96 hours whereas younger columns were composed in part of immature teliospores.

After sporidium production began, sporidia continued to be produced as long as weather conditions were favorable until the telial columns contained no more viable teliospores. A study of sporidium production during 24 consecutive hours was made under controlled environments of constant temperature and moisture. Heavily infected leaves of *Ribes nigrum* with an abundance of telial columns were removed from the bushes and immediately subjected to moisture and temperature conditions known to stimulate the production of sporidia. In each of 3 tests, a leaf was moistened with water and suspended in a damp chamber above the lower half of a petri dish that contained solidified water agar. The temperature was maintained at 65°F. At the end of each hour the petri dish was removed and a new dish of agar was set in the same position. In each petri dish, the surface of the agar that had been directly beneath the leaf was examined microscopically and the sporidia were counted in 4 separate microscopic fields, each with an area of approximately 1.54 sq. mm. The average of the 4 fields was recorded as the spore cast for that particular hour. The average spore count per hour from the 3 different leaves for the first 24 hours after sporidium production began was: first hour, 1 spore; second hour, 1.5 spores; third hour, 2 spores; fourth hour, 3 spores; fifth and sixth hour, 4 spores; seventh through the twelfth hours, 5 to 5.5 spores; thirteenth through the fifteenth hours, 4 to 4.5 spores; sixteenth and seventeenth hours, 6 spores; eighteenth to the twentieth hours, 4.5 to 5 spores; twenty-first through the twenty-third hours, 5.5 to 6.5 spores; twenty-fourth hour, 7.5 spores. Under the conditions of these tests sporidium production was continuous for 24 hours and the average spore cast was approximately the same after the sixth hour, although toward the close of the test the spore cast appeared to be increasing.

Under natural conditions, changes in the availability of free moisture, fluctuations of temperature and relative humidity, and variations in other factors commonly occur throughout 24-hour periods, and these changing factors affect sporidium production. In order to determine the effects of these changing factors, sporidium counts were made July 9 to 10 and 11 to 12, 1940, under natural weather

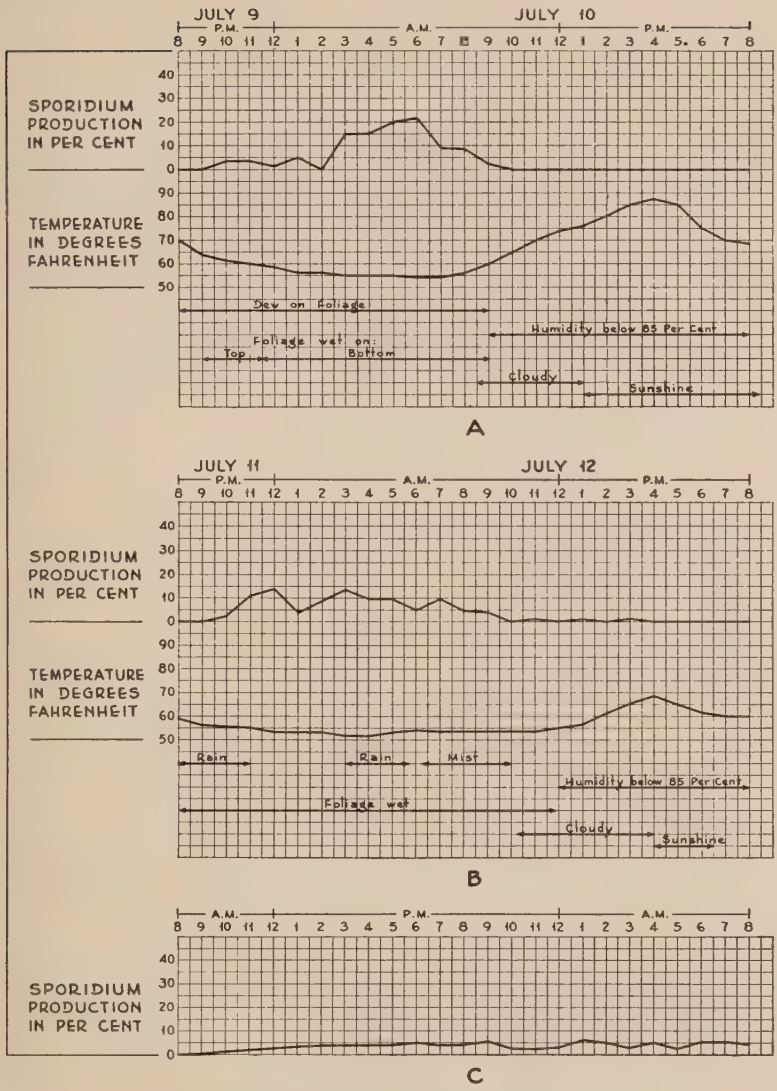


Fig. 4. A graphic summary of certain records for 1940 relating to sporidium production on leaves of *Ribes nigrum*. A and B. Sporidium production under natural conditions. C. Sporidium production from leaf sections kept under a favorable but non-fluctuating temperature and with free water continually available.

conditions. Without removing the leaves from the ribes bushes, each leaf under observation was held, by means of clamps and thumb tacks, in a horizontal position with the telium-bearing surface of the leaf down. Directly beneath these leaves open petri dishes of solidified water agar were placed on supports. These spore traps were changed hourly and spore counts were made from 5 microscopic fields in each petri dish. For comparison, spore counts were made from detached leaves kept under favorable moisture and a constant temperature of 55°F. for 24 hours, as previously described. The results are shown in figure 4. The changing meteorological conditions definitely produced marked variations in the spore cast. The absence of free moisture appeared to be one of the most detrimental factors to the production of sporidia, although a few sporidia were produced during the cloudy interval, July 12, when free water was no longer present. Under the constant temperature and continuous supply of moisture in the control chambers (Fig. 4, C), sporidium production continued to the termination of the test; the spore cast was relatively even during the 24 hours. Most of the sporidia that fell upon the agar in the spore traps had the characteristics of secondary sporidia, that is, they did not produce other sporidia but sent out 2 to 5 germ tubes that continued to elongate while conditions for growth were favorable. Each hour several petri dish spore traps had their covers replaced after sporidia were caught and the dishes were set beneath the ribes bushes so as to subject them to the prevailing outdoor temperatures. By 10 A.M., 12 hours after the first spores were cast, the maximum length of the germ tubes was 20 μ, which was about sufficient for the tubes to extend through the epidermis of a pine needle either directly or indirectly by way of the stomata (7), but probably not sufficiently long to permit establishment in the mesophyll tissue and bring about needle infection.

Observations made throughout the years of this study have disclosed that, when the fungus and ribes leaves were in proper condition for teliospore development, telial columns continued to be produced during periods that were favorable for the production of sporidia as well as during almost all of the other usual weather conditions that existed throughout the summer and early autumn. The telial columns elongated quite slowly and during extended periods with weather conditions advantageous for sporidium production new teliospores were formed less rapidly than the mature teliospores germinated, so that a time would come when the older telial columns were exhausted or nearly so and the younger columns were not long enough to contain many viable mature teliospores. Consequently the number of sporidia was reduced to such an extent as to allow very little opportunity for infection of the pines. Such a state of teliospore exhaustion would be reached quickly unless the fungus was especially active in producing teliospores. The period between August 20 and September 5, 1927 (Table 1) probably illustrates an interval of de-

TABLE 1.—INFECTION OF WHITE PINE BY THE BLISTER-RUST FUNGUS DURING 17 DAYS OF AUGUST IN 1927. TWENTY POTTED PINES WERE EXPOSED TO TELIUM-BEARING BUSHES OF RIBES NIGRUM DAILY FOR 24 HOURS, BEGINNING AT 8 A.M. EACH DAY

Date of exposure	Rainfall in inches	Hours with relative humidity of 85 per cent or higher	Temperature range in degrees Fahrenheit by hours				No. of trees infected	No. of infections
			40°-49°	50°-65°	66°-69°	70°+		
Aug.								
20	0.00	15	0	15	3	6	1	2
21	0.00	15	0	14	1	9	2	3
22	0.00	14	0	14	2	8	3	3
23	0.03	14	0	0	13	11	6	7
24	0.10	18	0	14	8	2	1	1
25	0.00	10	10	6	5	3	8	19
26	0.00	12	0	17	3	4	13	38
27	0.50	24	0	24	0	0	19	312
28	0.80	24	0	24	0	0	17	123
29	0.48	18	0	14	10	0	14	39
30	0.21	18	0	18	5	1	17	39
31	0.06	21	0	14	4	6	13	27
Sept.								
1	0.41	19	0	14	6	4	15	26
2	0.11	24	0	14	10	0	6	6
3	0.00	16	0	12	4	8	1	1
4	0.00	8	0	13	4	7	0	0
5	0.00	11	9	9	2	4	1	1

creased sporidium production because of near teliospore exhaustion. In that year the pines were exposed to telium-bearing ribes for 24 hours per day, from 8 A.M. to 8 A.M. Almost every day from August 1, some infection took place but extended intervals of favorable weather did not occur until August 27. The weather on August 27 and 28 was almost identical and apparently ideal for teliospore germination, but the number of infections on the second day, August 28, was less than 40 per cent of the number during the preceding day. Although the weather did not change greatly during the 5 succeeding days, the number of infections was greatly reduced. It seems reasonable to assume that the reduction in the number of infections was definitely the result of a decreased supply of sporidia due to teliospore exhaustion.

Temperature influence.—Temperature has been demonstrated to be an important factor governing the production of sporidia (5, 20). Tests conducted under controlled environments indicated the cardinal temperature range to be approximately 50°F. to 65°F. and the mini-

mum and maximum temperatures approximately 32° F. and 70° F., respectively. The field experiments under natural meteorological conditions supported these conclusions (Figs. 5 to 11, inclusive). The damp-chamber plants demonstrate this fact even better than the pines exposed wholly to the natural meteorological environment because, in addition to being present in the ribes garden, immediately after exposure these pines were placed in the damp chamber for 36 hours and subjected to a temperature and humidity favoring pine infection. The presence of infection on the damp-chamber trees and the absence of infection on the pines exposed to inoculation at the same time but subjected only to natural weather show that sporidia were often produced under natural conditions when weather factors did not permit needle infection. Figures 12, 15, 26, 30, and 31 show the temperature ranges in some detail during several of the 12-hour periods when sporidia were present, as demonstrated by infections on the damp-chamber pines, but when infection did not occur under natural conditions. The sporidia were produced mostly under temperatures previously demonstrated by controlled conditions to be optimum for the fungus.

The scope of the cardinal temperature range is so broad that throughout the natural range of eastern white pine, these temperatures are apt to occur at the same time that other meteorological factors are favorable to sporidium production.

Moisture influence.—Moisture, available either as water vapor or free water, is essential to sporidium production. Pine infection recorded in figures 5 to 11 indicate that the production of sporidia was restricted almost wholly to days with rain or hours of darkness when the relative humidity was high. In the experimental areas, it was found that when a relative humidity of 85 per cent or more existed, free water was present on the foliage as a result of rain, fog, or dew. The relative effects of these moisture conditions will be discussed subsequently in regard to pine infection.

Sporidium germination.—Pine infection is dependent upon the germination of sporidia as well as upon other factors. Previous studies (5, 20) have contributed certain valuable information regarding some of the factors that influence the process of germination in a controlled environment. The following statements briefly summarize the more important points. Free water, or a relative humidity of at least 97 per cent, is essential for the germination of sporidia. Sporidia germinate at temperatures of approximately 32° F. to 70° F.; at temperatures of roughly 50° F. to 65° F. secondary sporidia are formed. These secondary sporidia almost invariably produce true infection hyphae when kept at the same temperatures and in the same moisture conditions under which they were formed. Alternate drying and wetting decrease the viability of sporidia. Some sporidia were found to retain their viability for 26 hours on glass slides when

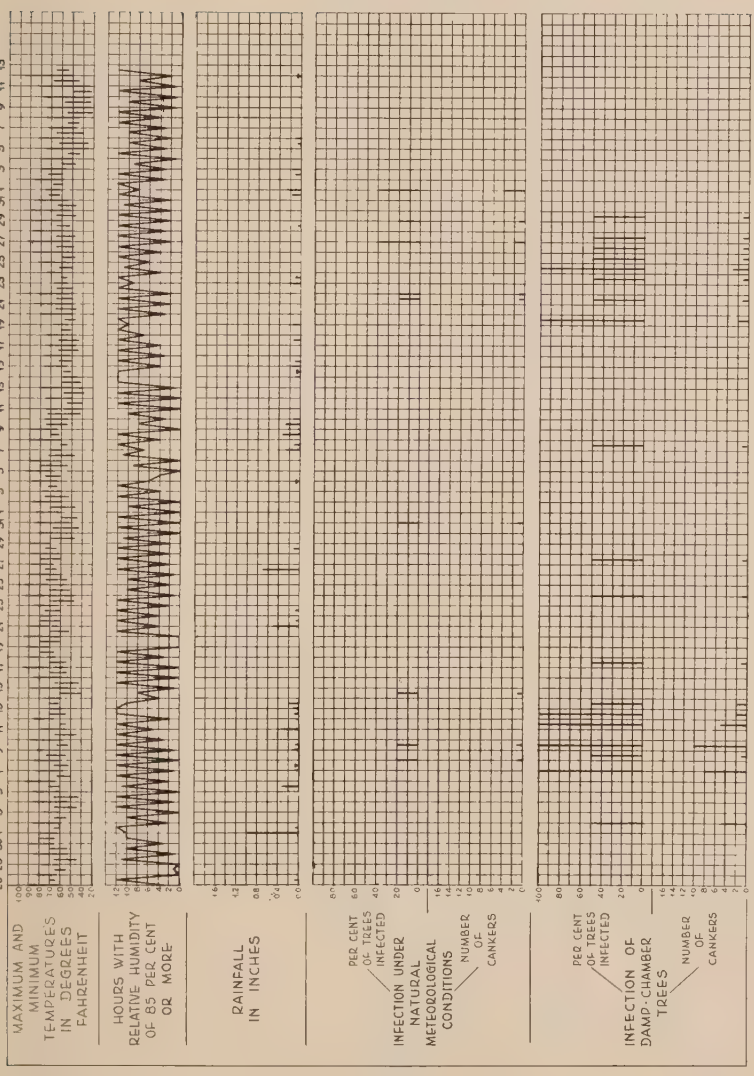


Fig. 5. A graphic summary of certain records for 1930 relating to sporidium production and white pine infection. The dated lines represent the time from 8:00 A.M. to 8:00 P.M. of that day; the following space represents 8:00 P.M. to 8:00 A.M. In the rainfall records, T signifies a trace.

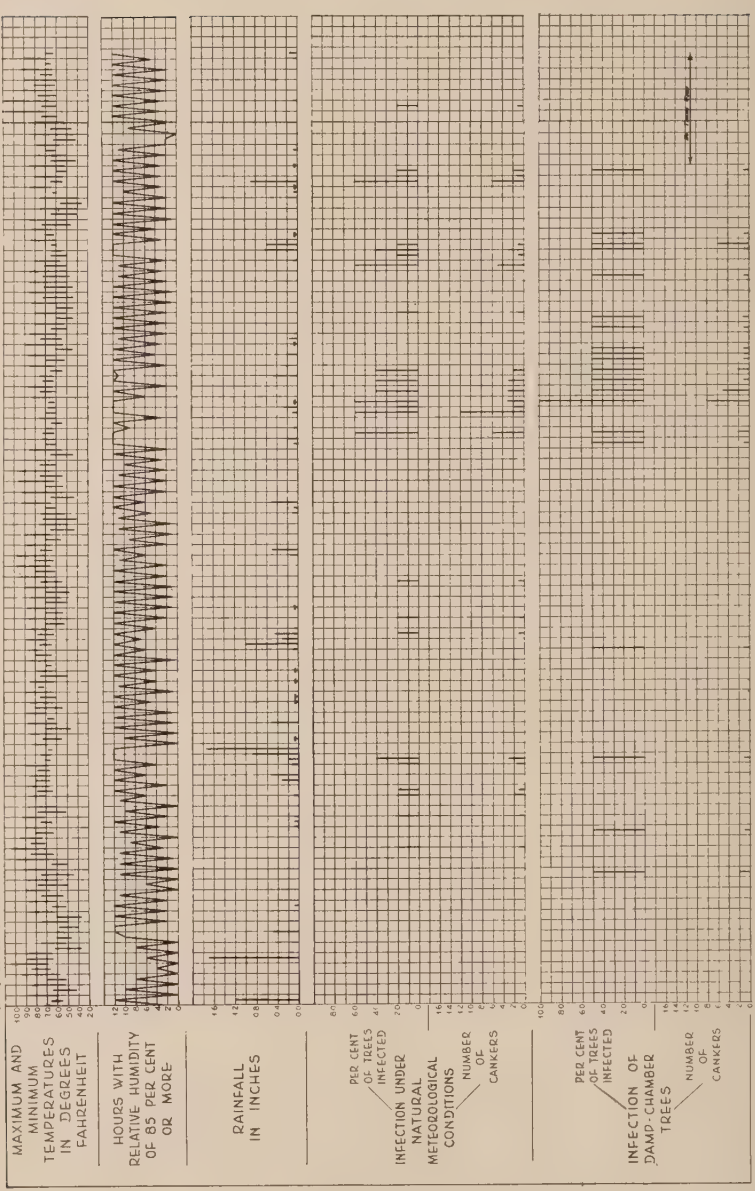


Fig. 6. A graphic summary of certain records for 1931 relating to sporidium production and white pine infection. The dated lines represent the time from 8:00 A.M. to 8:00 P.M. of that day; the following space represents 8:00 P.M. to 8:00 A.M. In the rainfall records, T signifies a trace.

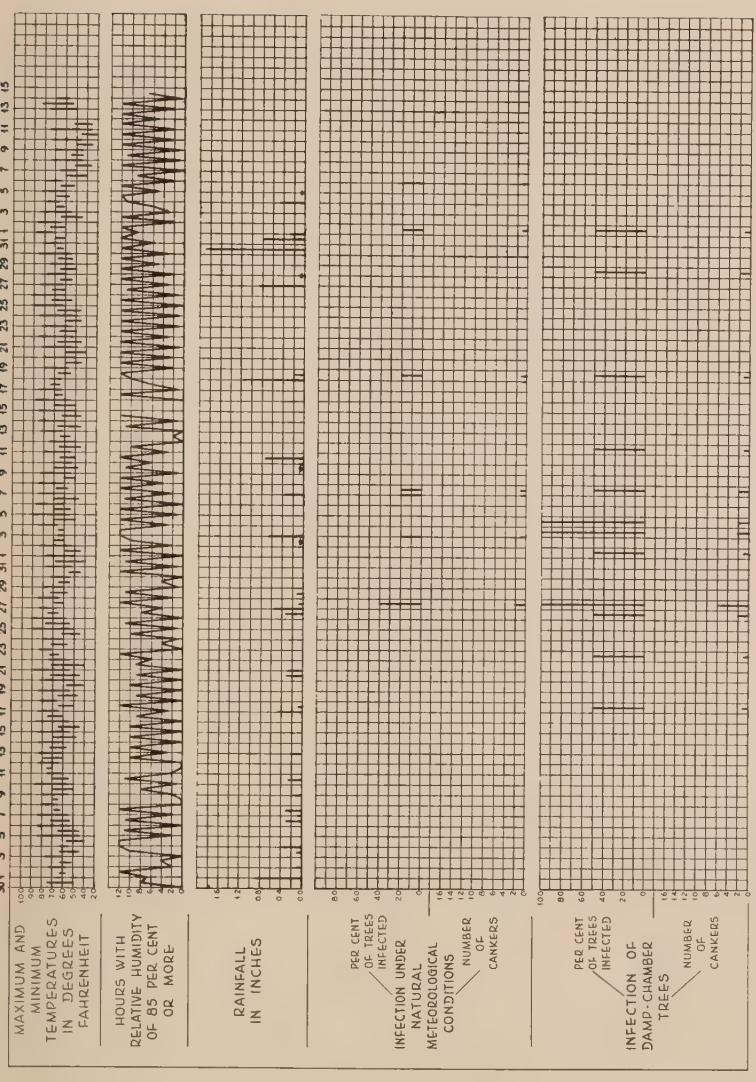


Fig. 7. A graphic summary of certain records for 1932 relating to sporidium production and white pine infection. The dated lines represent the time from 8:00 A.M. to 8:00 P.M. of that day; the following space represents 8:00 P.M. to 8:00 A.M. In the rainfall records, T signifies a trace.

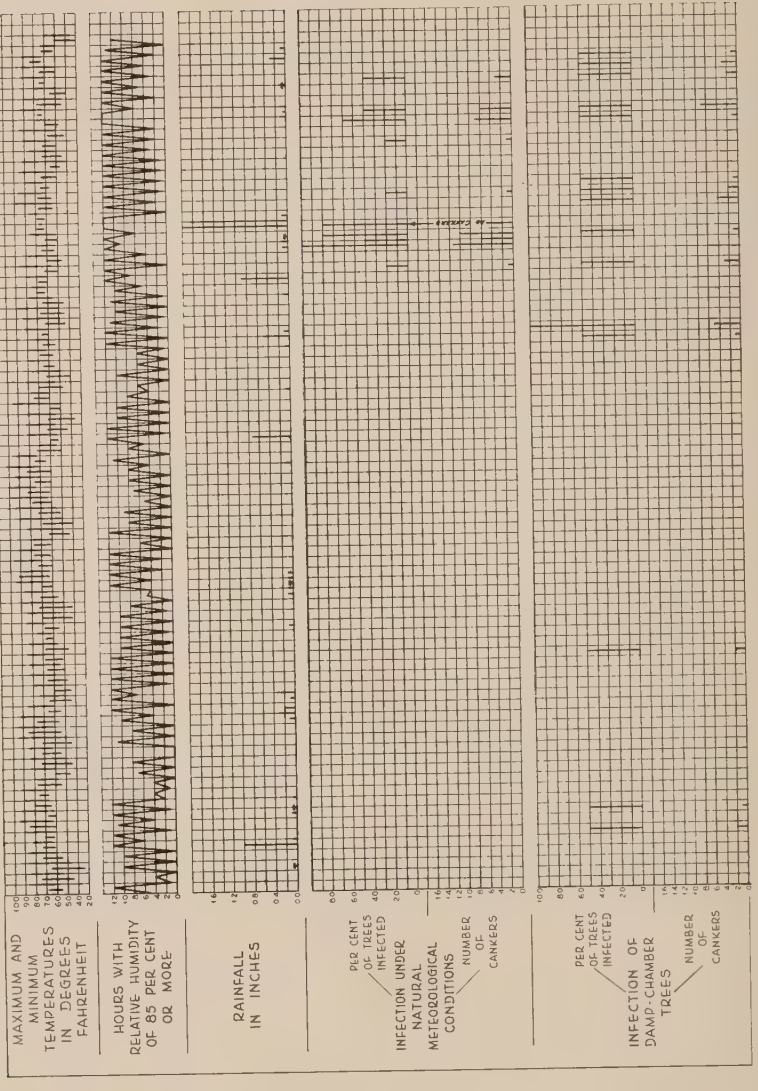


Fig. 8. A graphic summary of certain records for 1933 relating to sporidium production and white pine infection. The dated lines represent the time from 8:00 A.M. to 8:00 P.M. of that day; the following space represents 8:00 P.M. to 8:00 A.M. In the rainfall records, T signifies a trace.

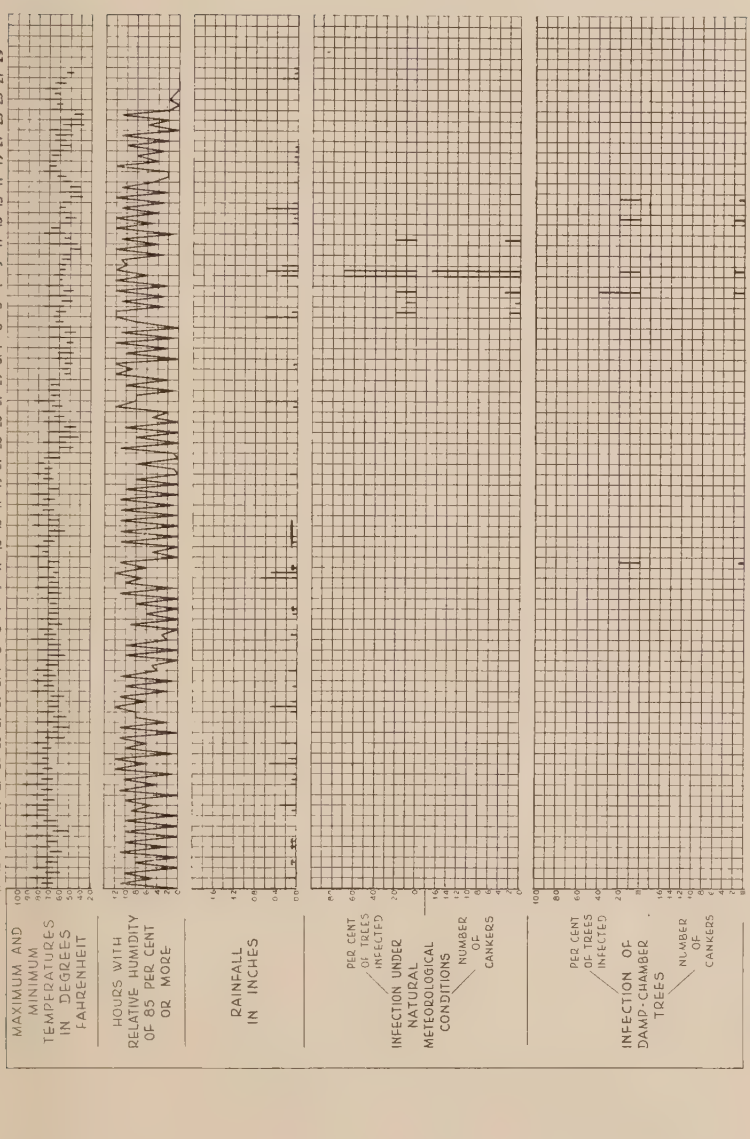


Fig. 9. A graphic summary of certain records for 1935 relating to sporidium production and white pine infection. The dated lines represent the time from 8:00 A.M. to 8:00 P.M. of that day; the following space represents 8:00 P.M. to 8:00 A.M. In the rainfall records, T signifies a trace.

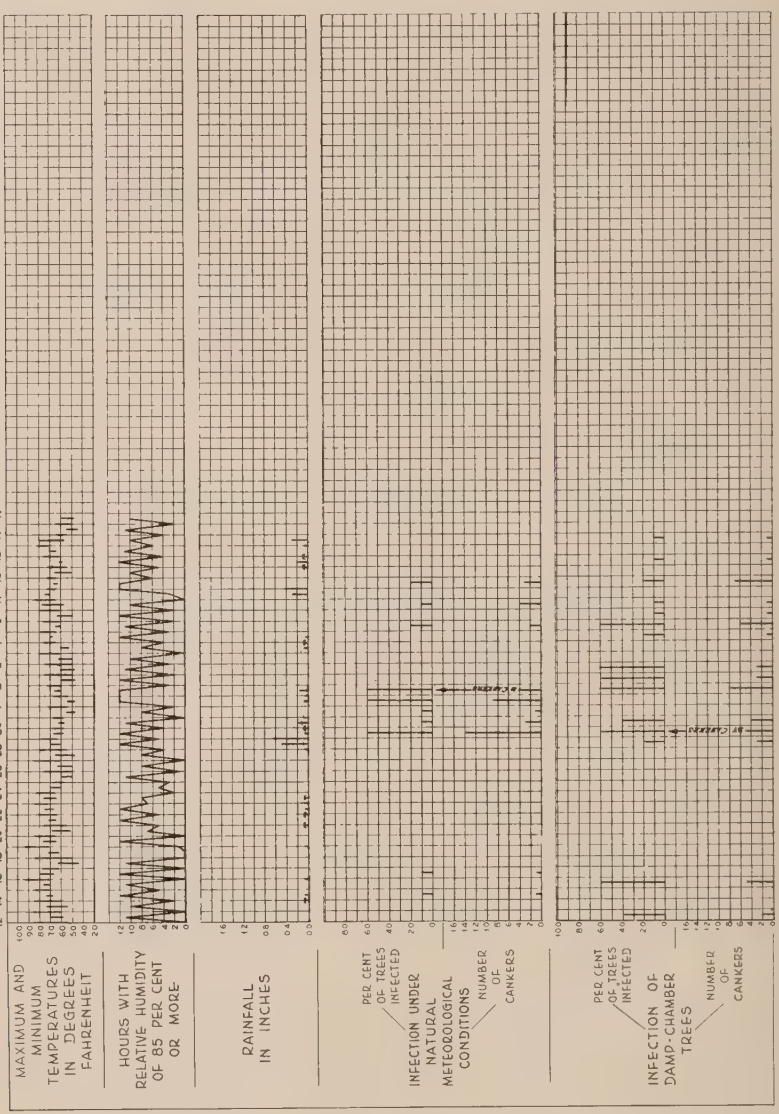
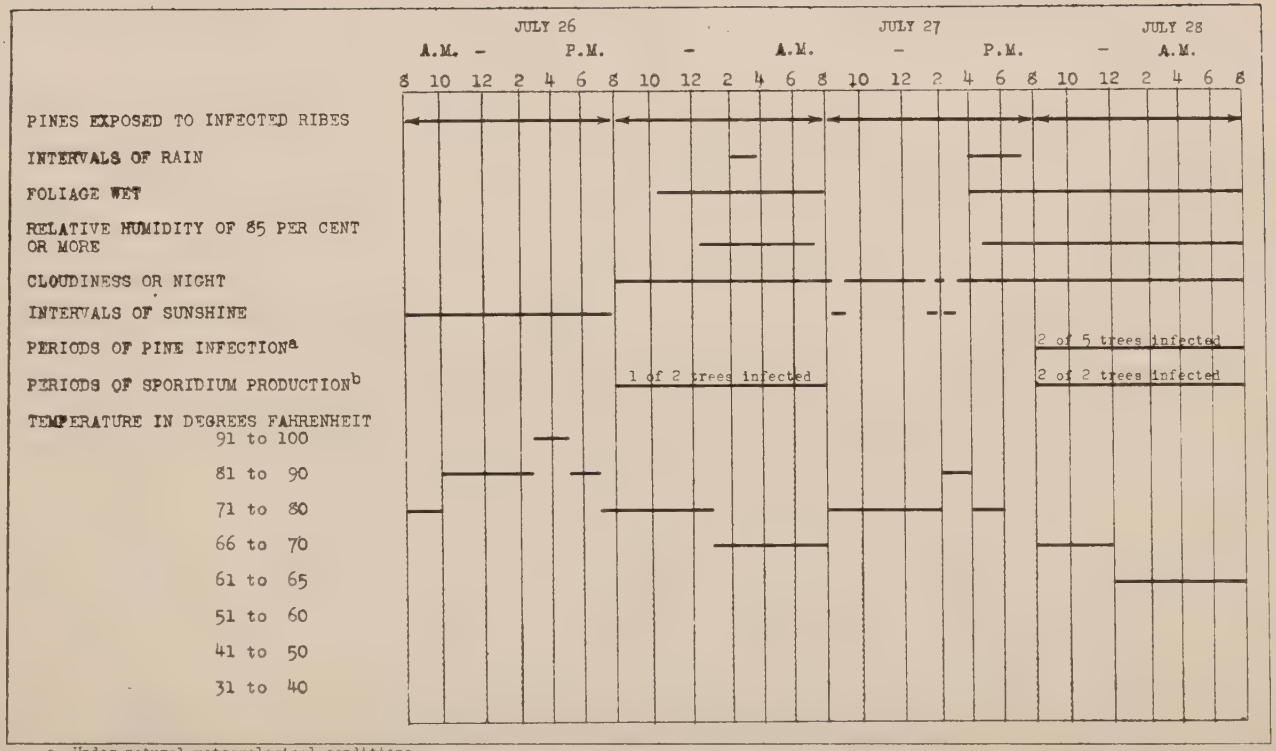


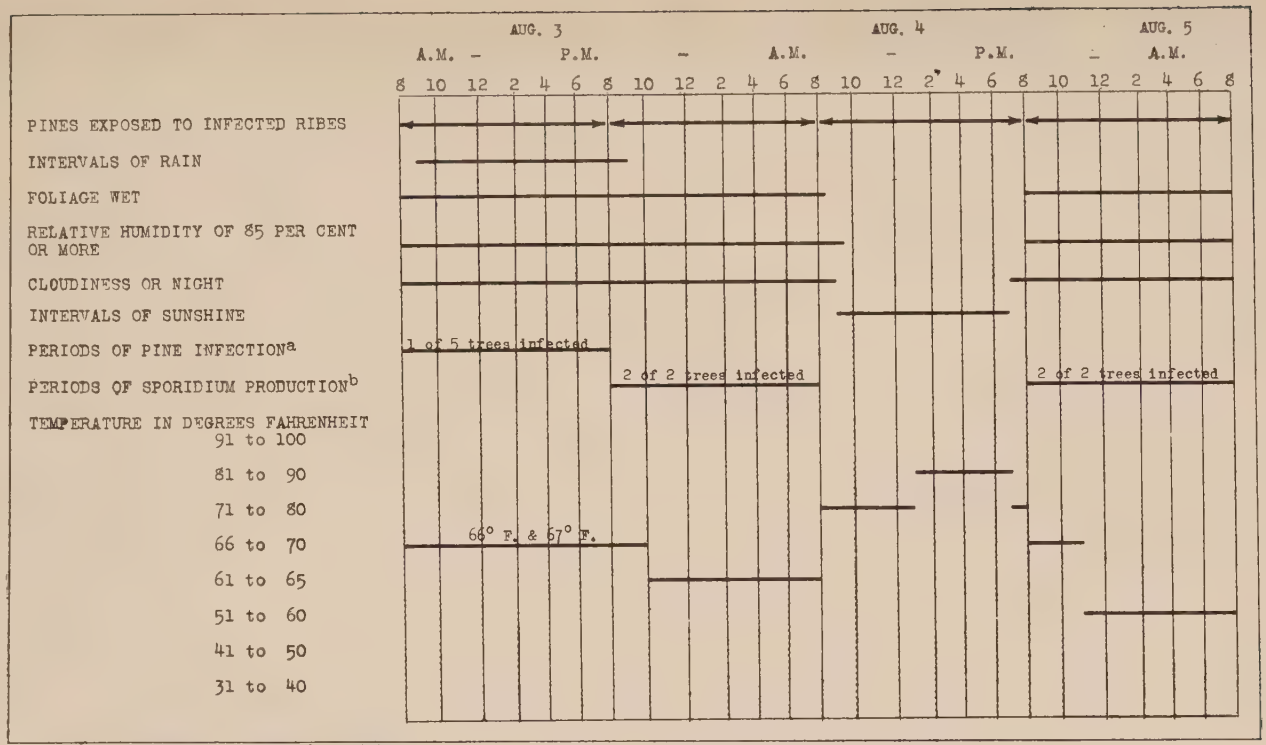
Fig. 10. A graphic summary of certain records for 1936 relating to sporidium production and white pine infection. The dated lines represent the time from 8:00 A.M. to 8:00 P.M. of that day; the following space represents 8:00 P.M. to 8:00 A.M. In the rainfall records, T signifies a trace.

Fig. 11. A graphic summary of certain records for 1937 relating to sporidium production and white pine infection. The dated lines represent the time from 8:00 A.M. to 8:00 P.M. of that day; the following space represents 8:00 P.M. to 8:00 A.M. In the rainfall records, T signifies a trace.



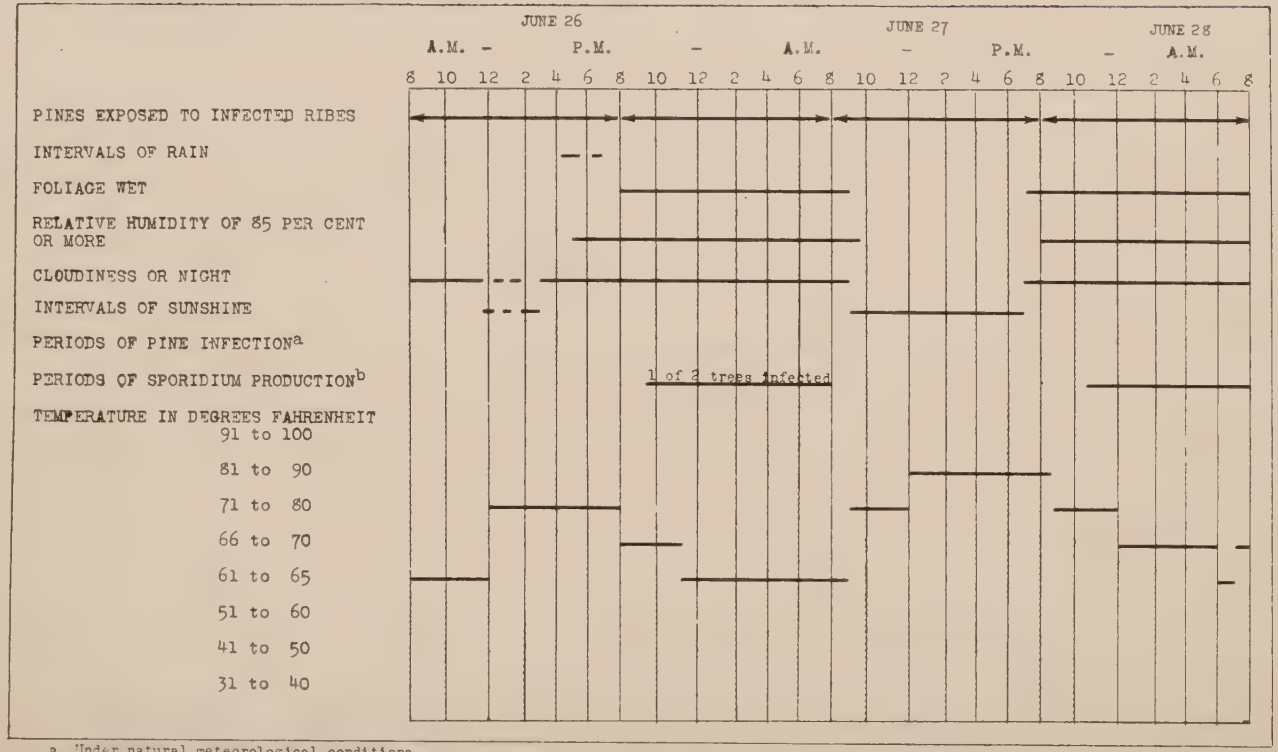
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 12.- Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1932.



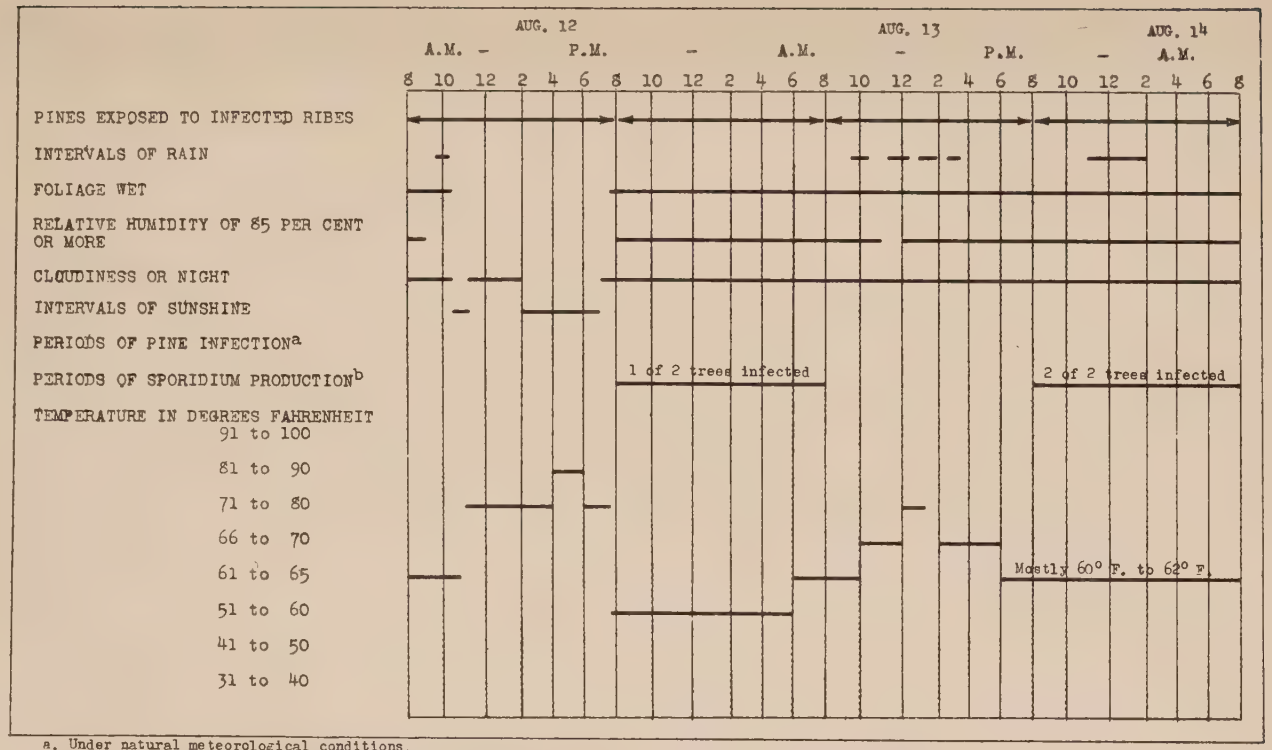
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 13. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1932.



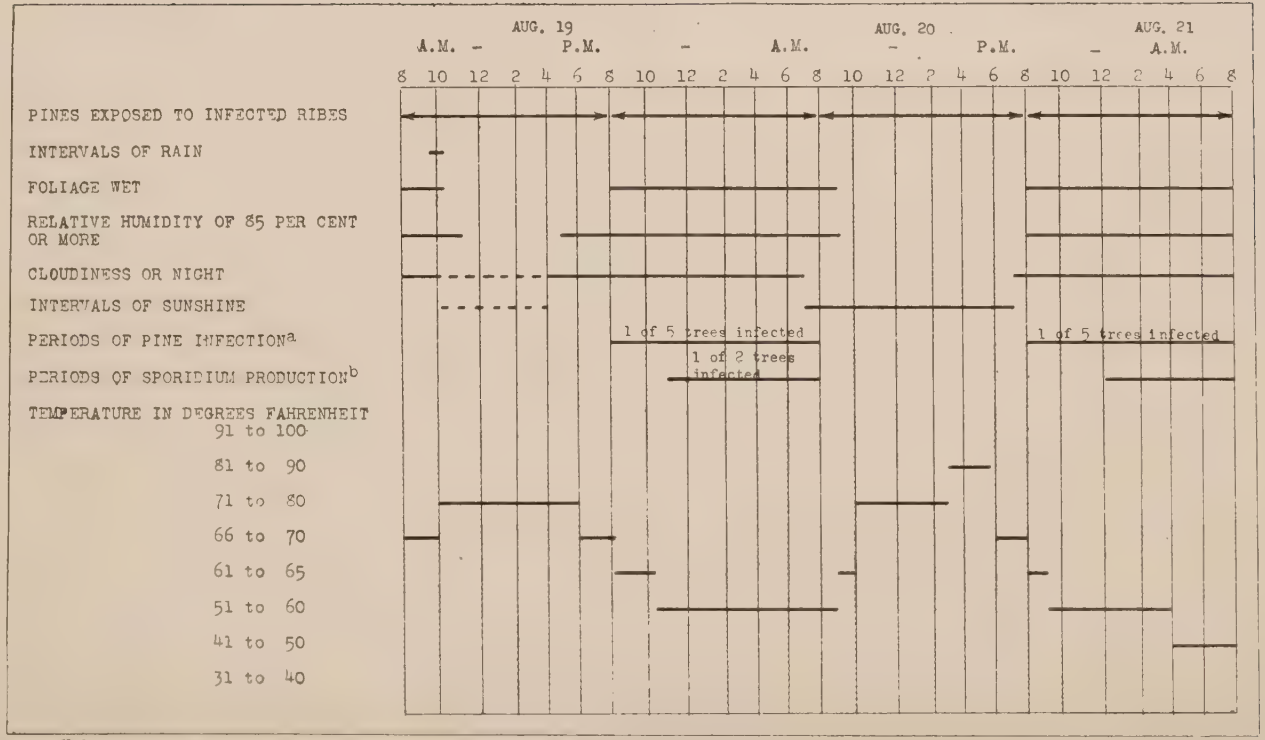
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 14. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



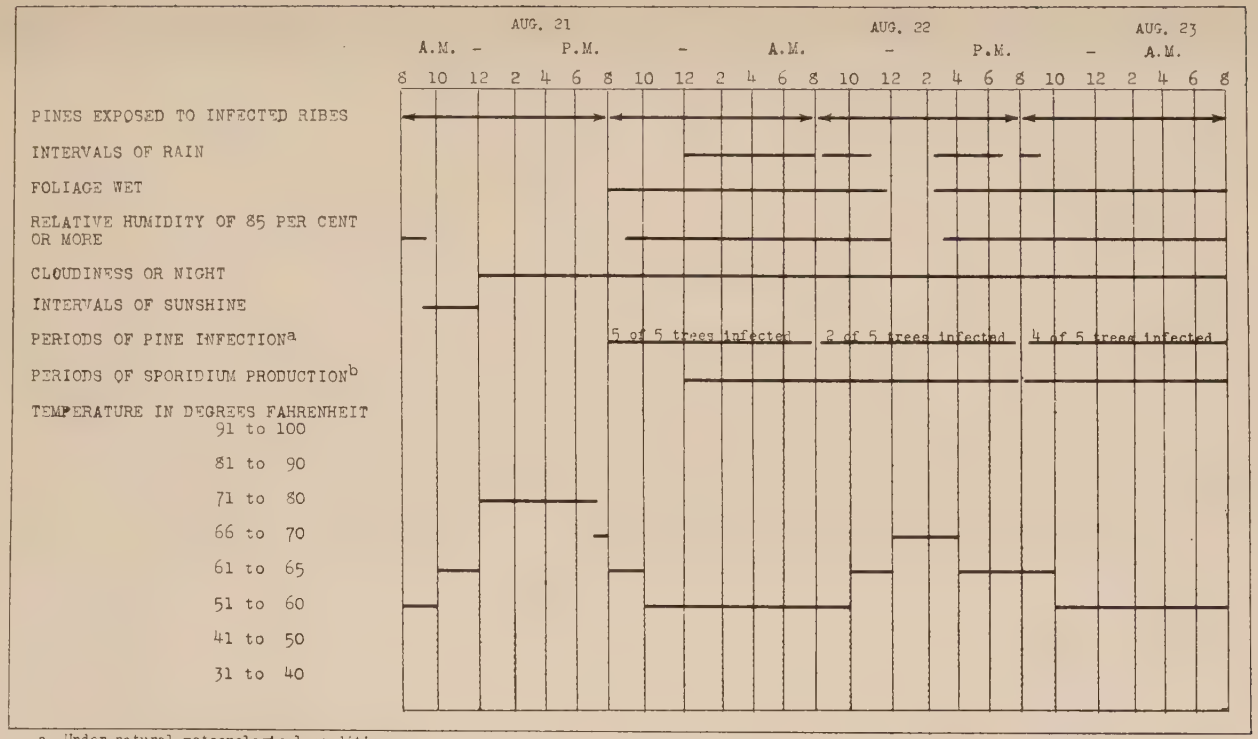
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 15. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



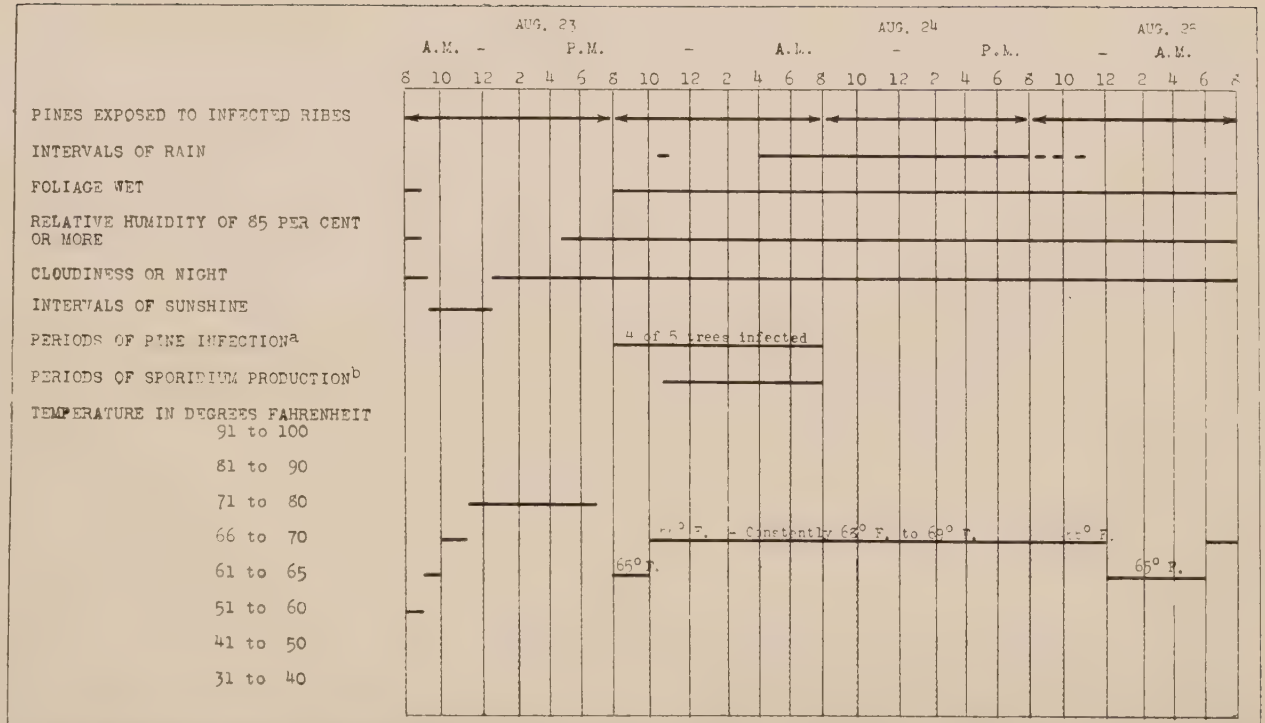
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 16. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



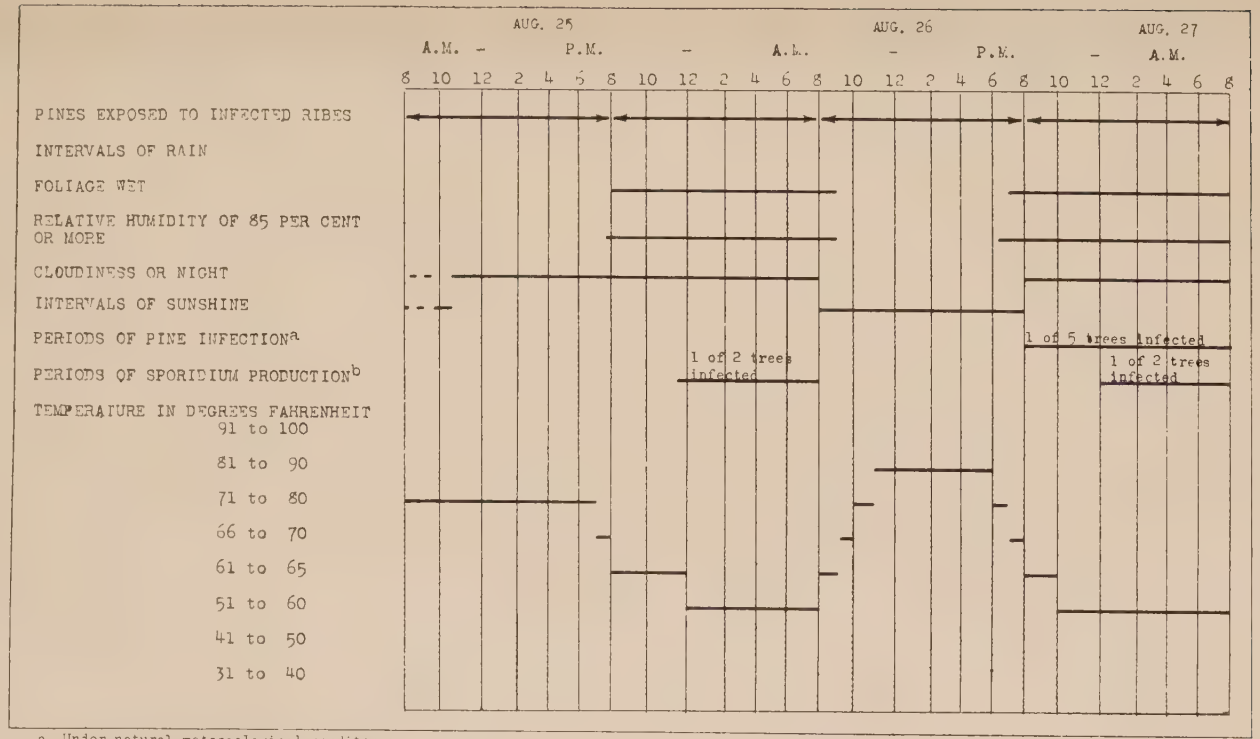
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 17. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



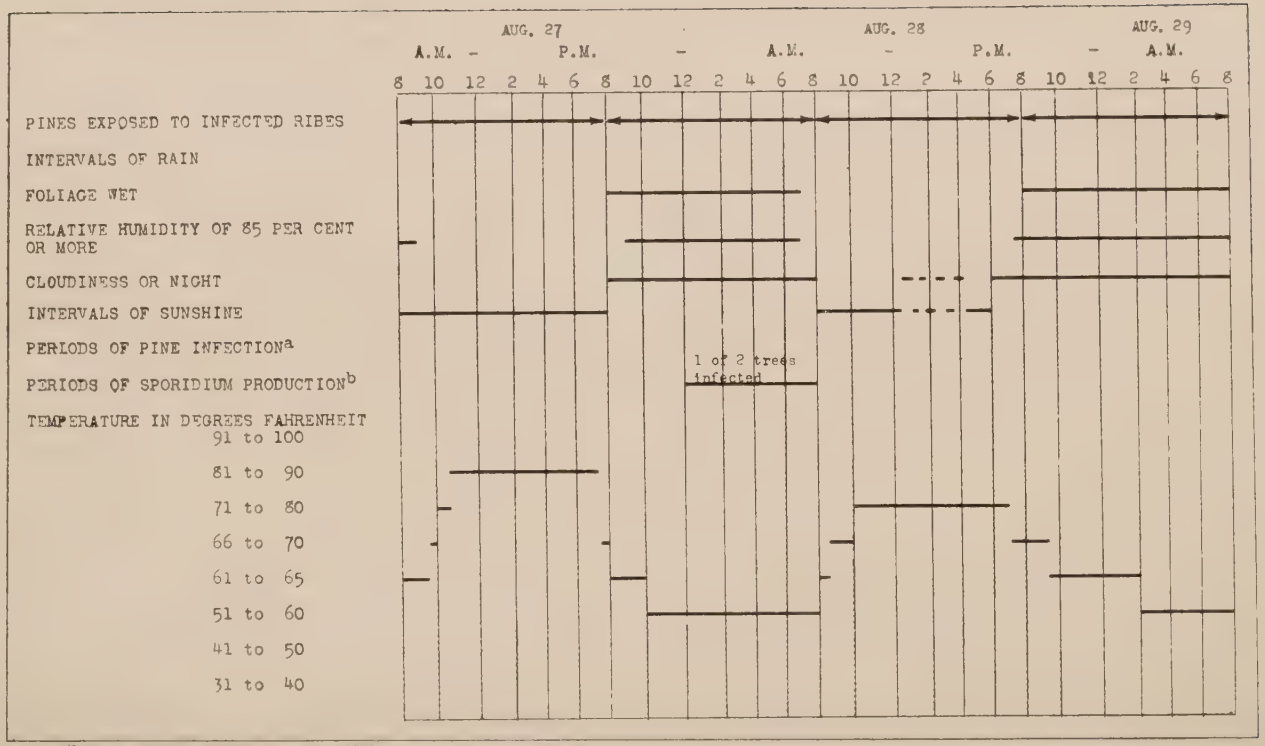
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of dampchamber trees and trees exposed to natural conditions.

Fig. 18. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



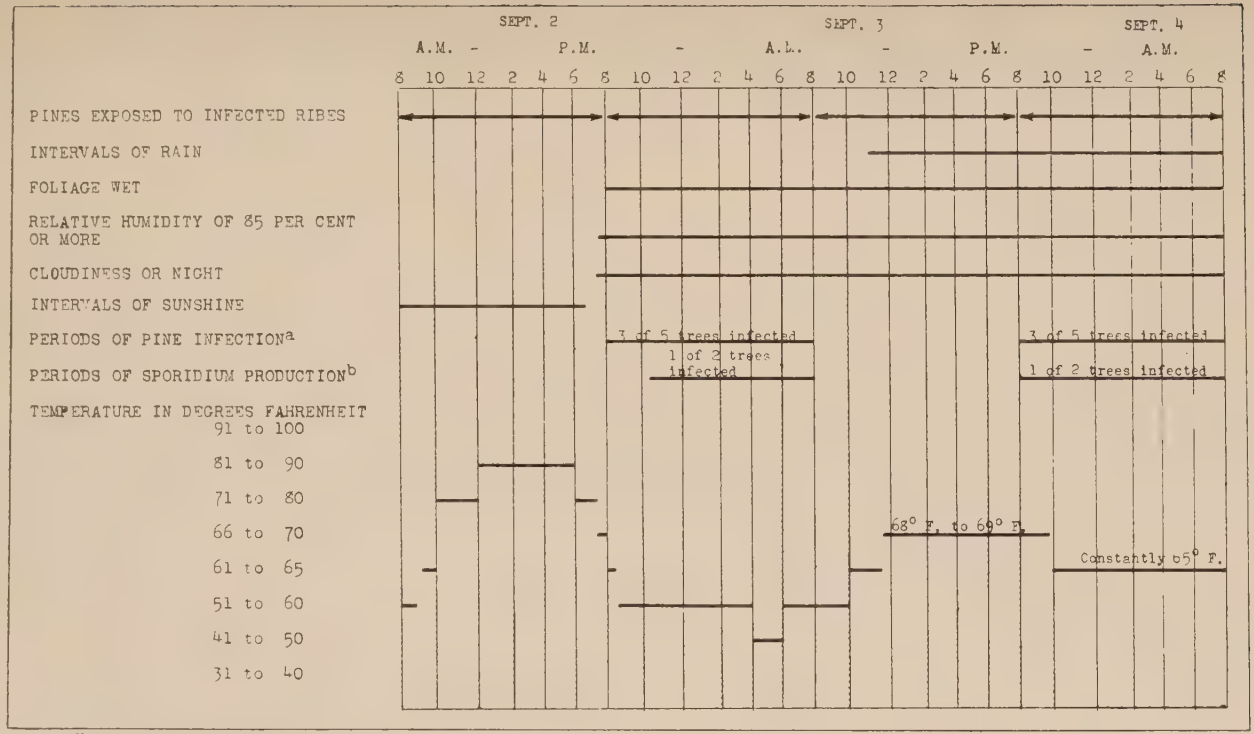
a. Under natural meteorological conditions.
b. Shown by microscopical studies, infection of dame-chamber trees and trees exposed to natural conditions.

Fig. 19. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



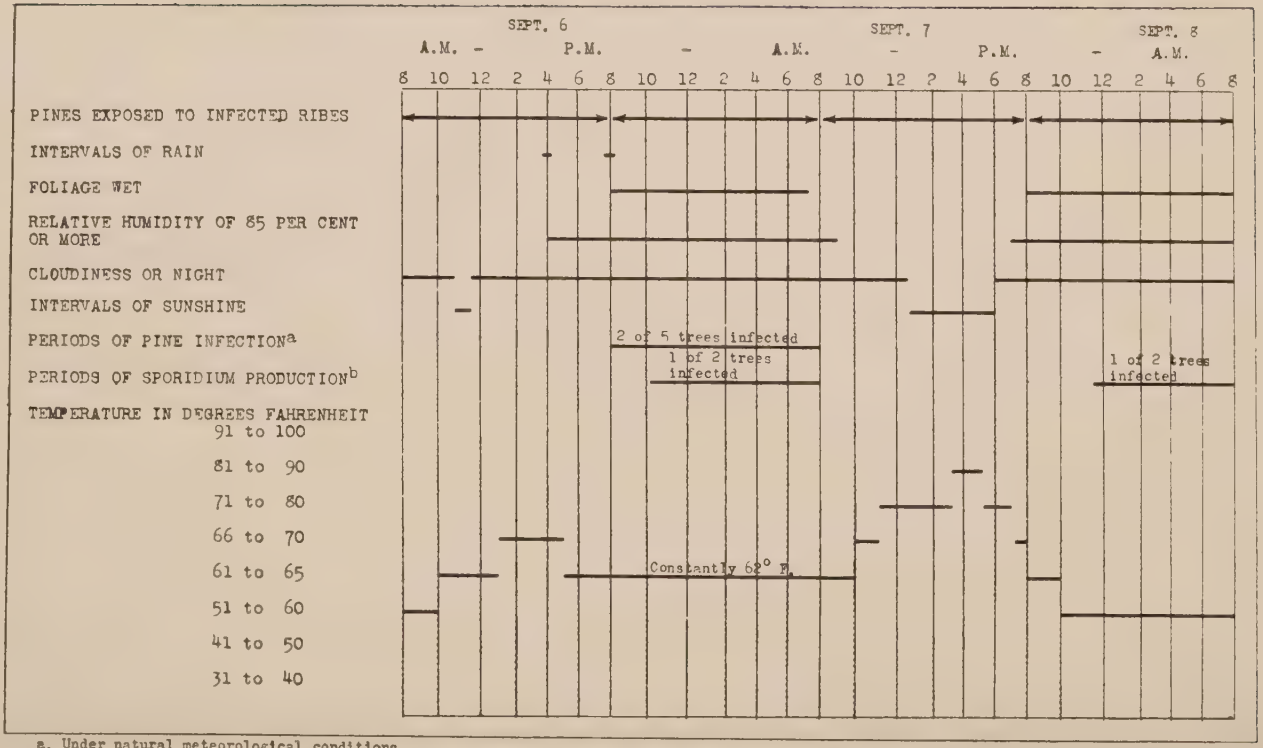
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 20. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



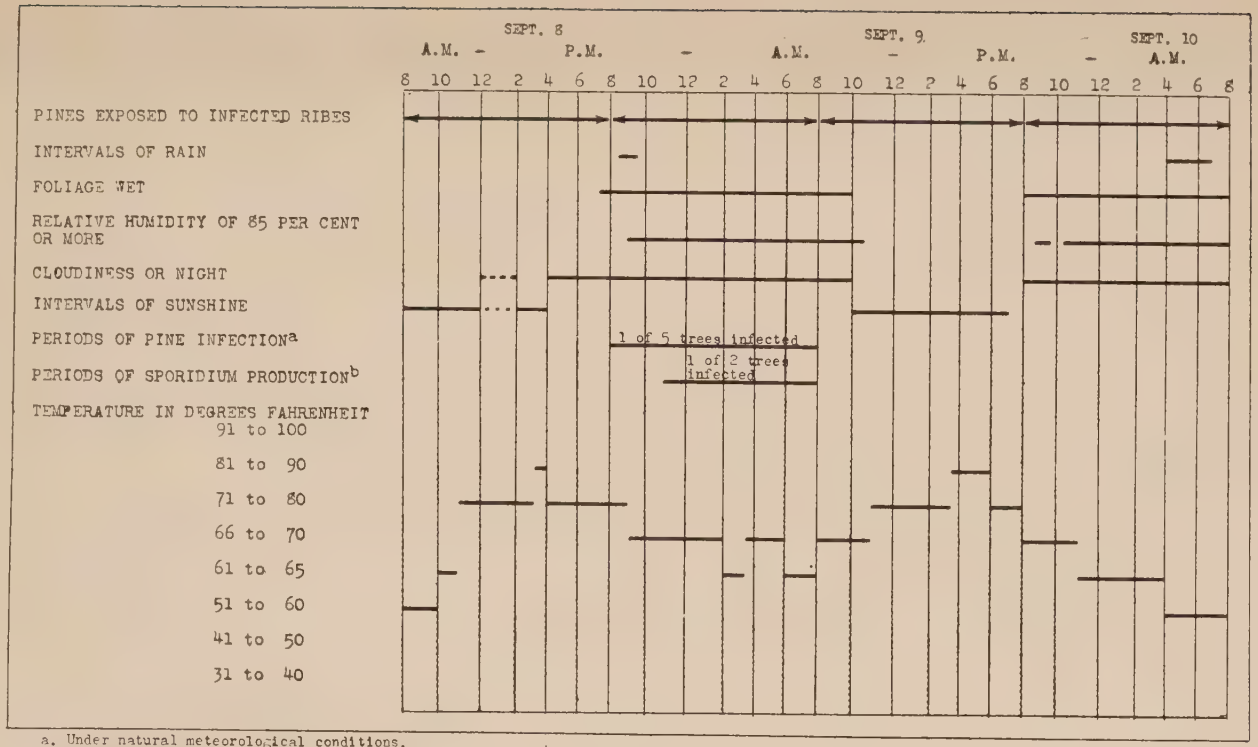
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of dame-chamber trees and trees exposed to natural conditions.

Fig. 21. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933



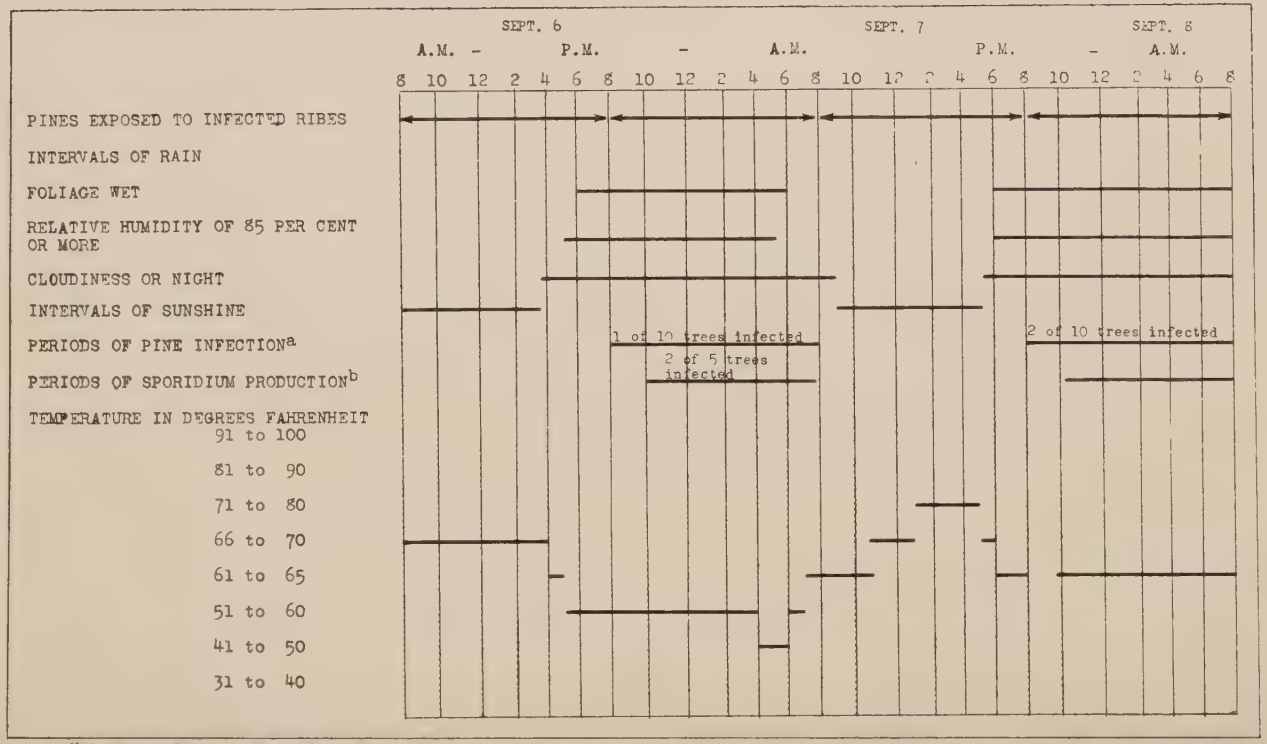
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 22. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



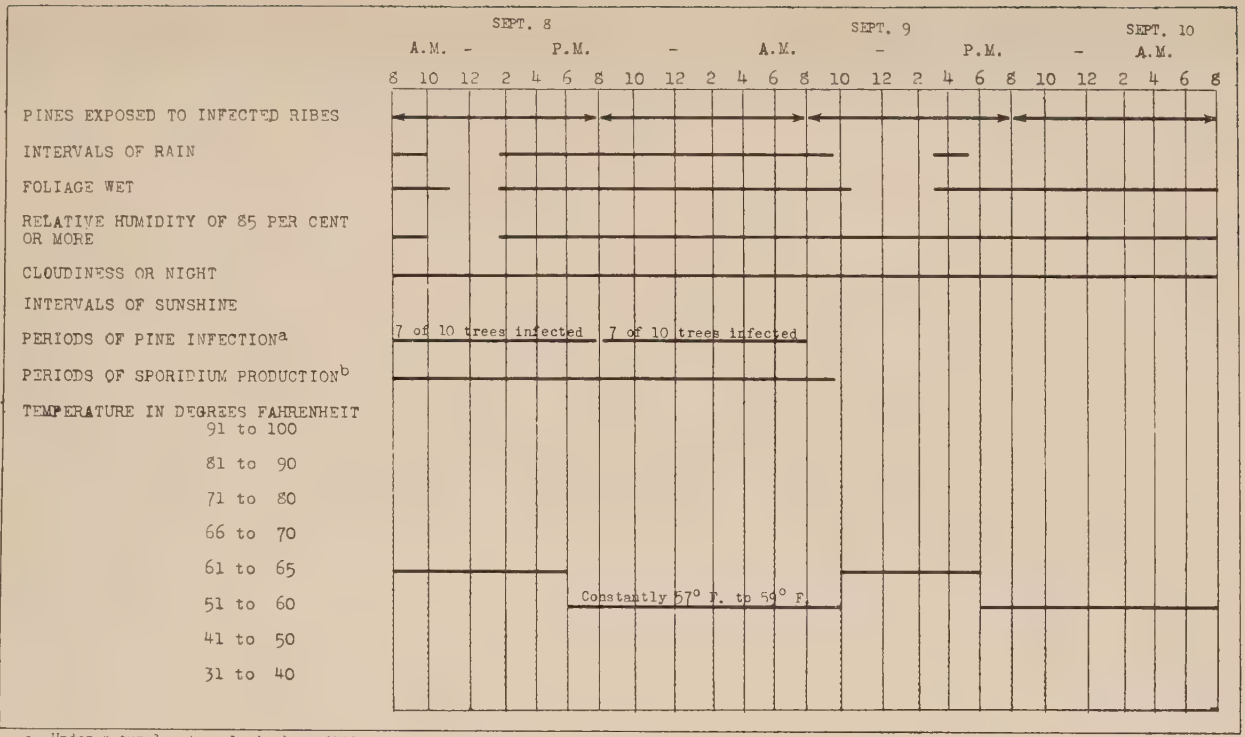
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 23. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1933.



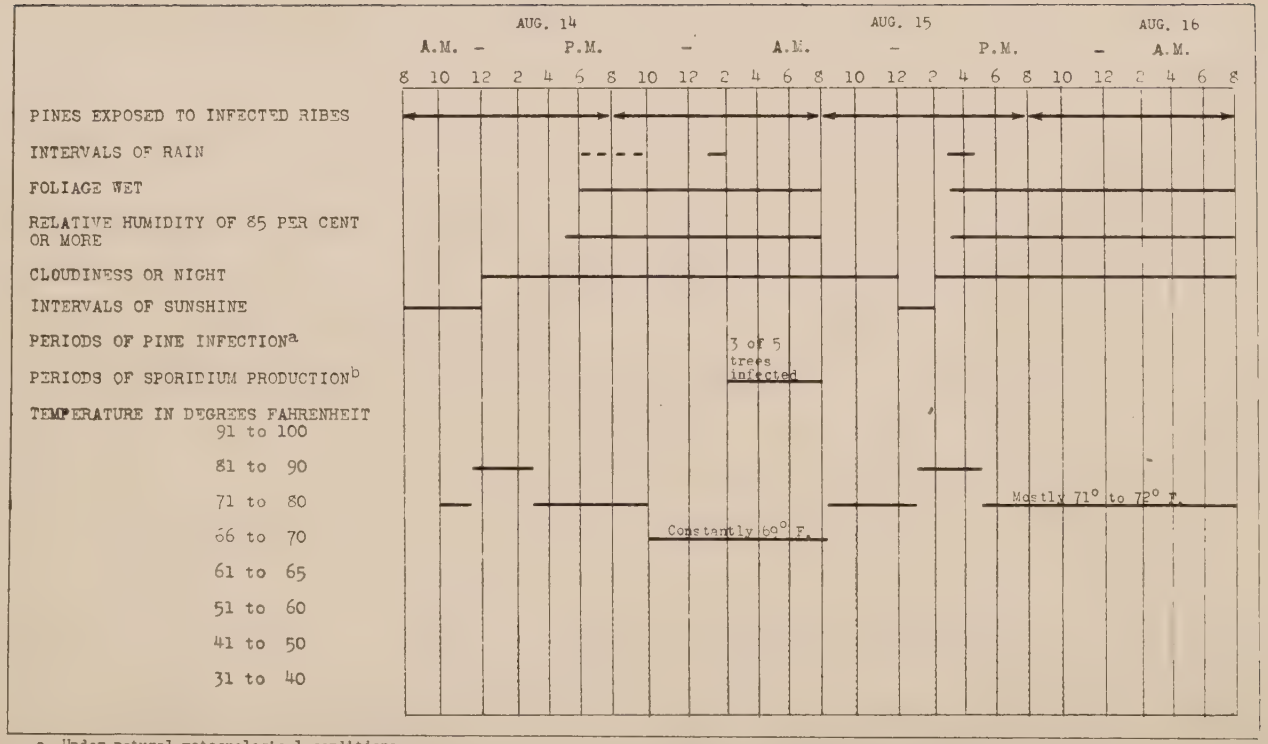
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 24. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1935.



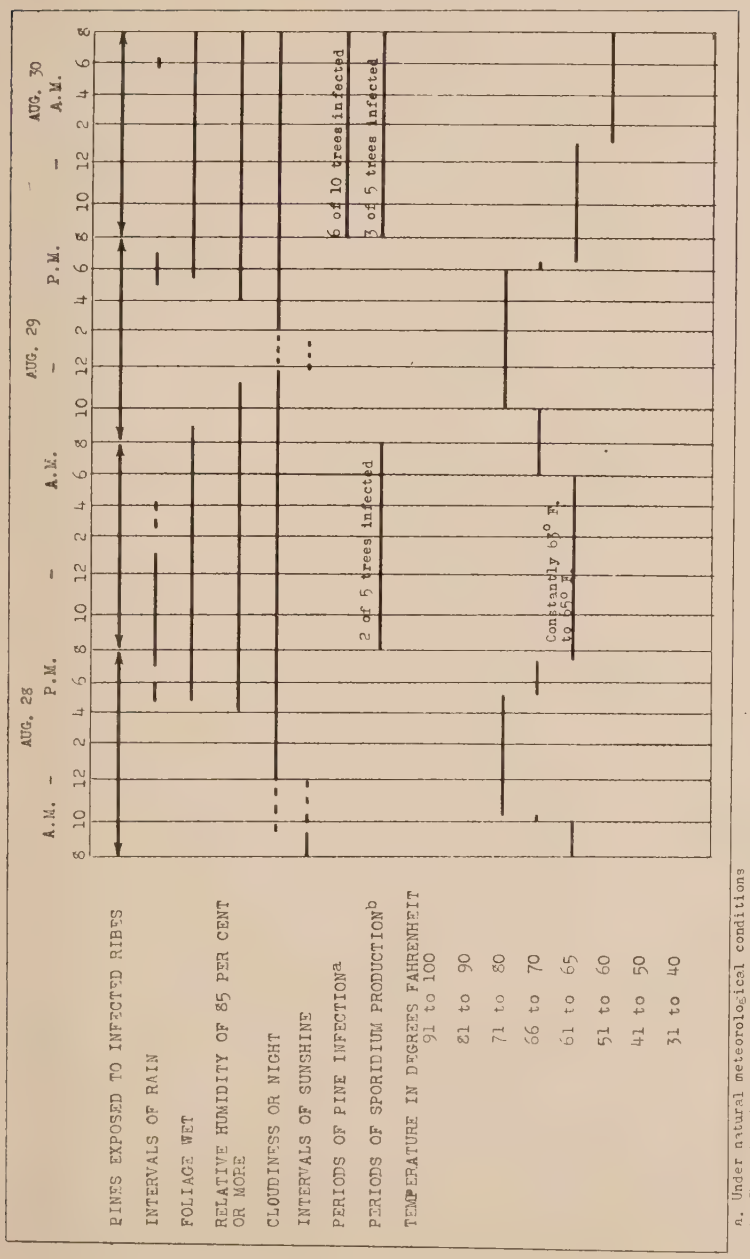
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 25. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1935.



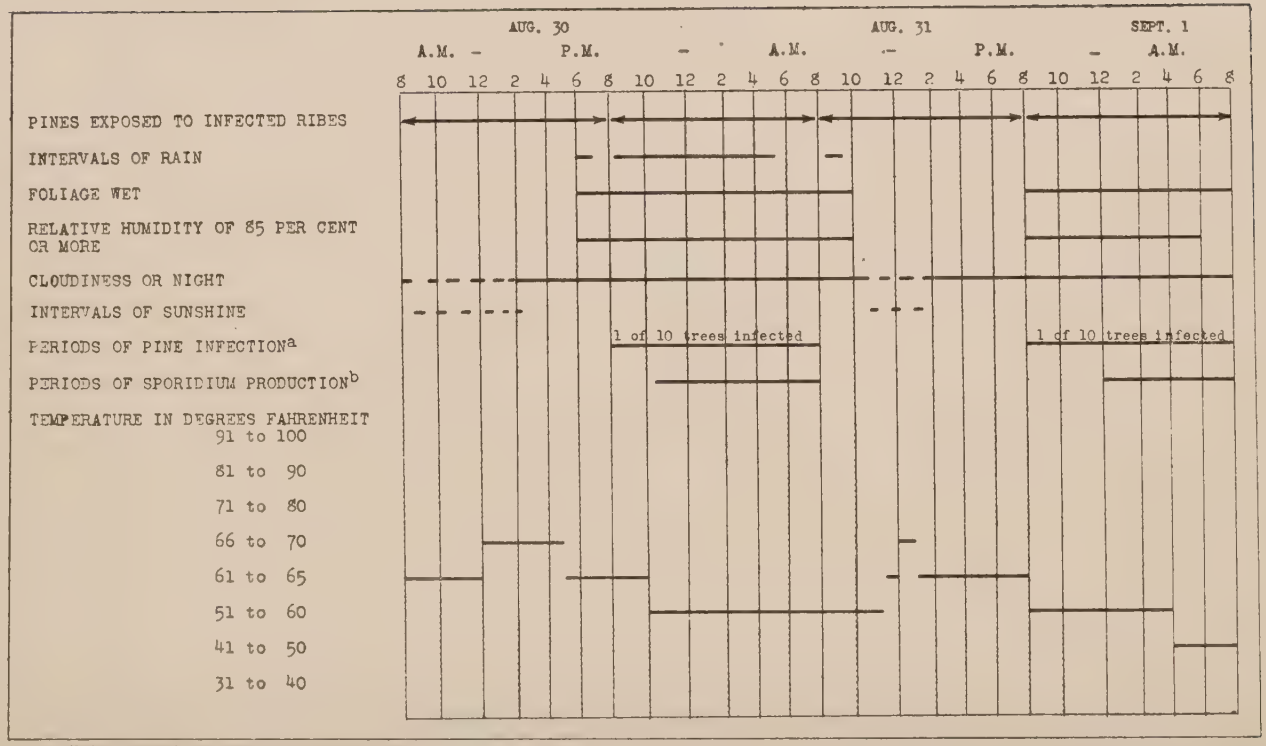
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 26. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1936.



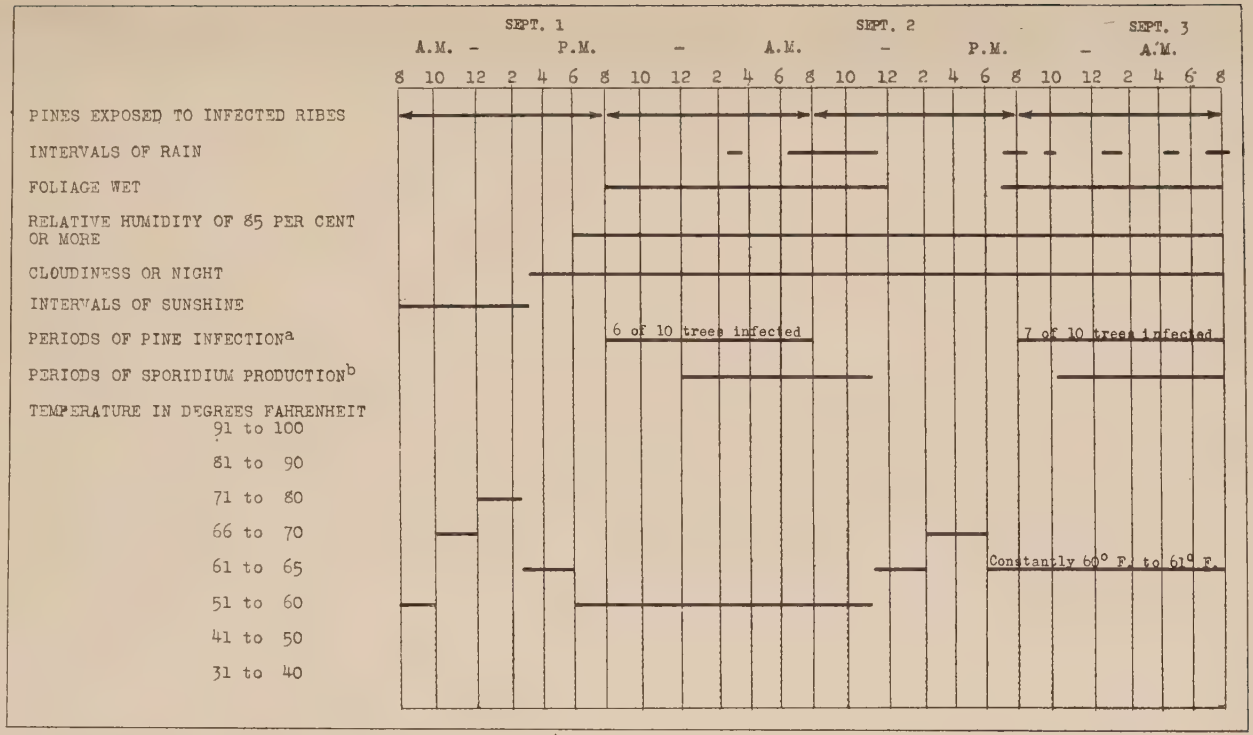
a. Under natural meteorological conditions
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 27. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1936.



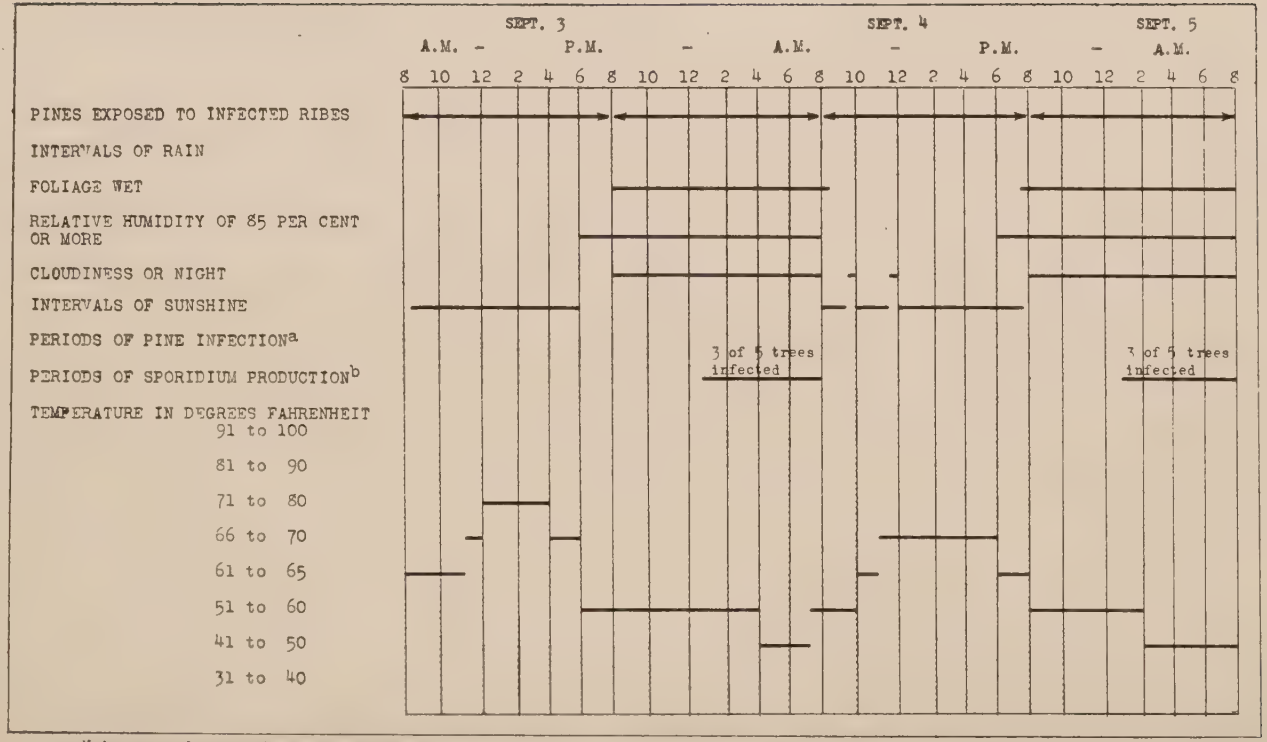
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 28. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1936.



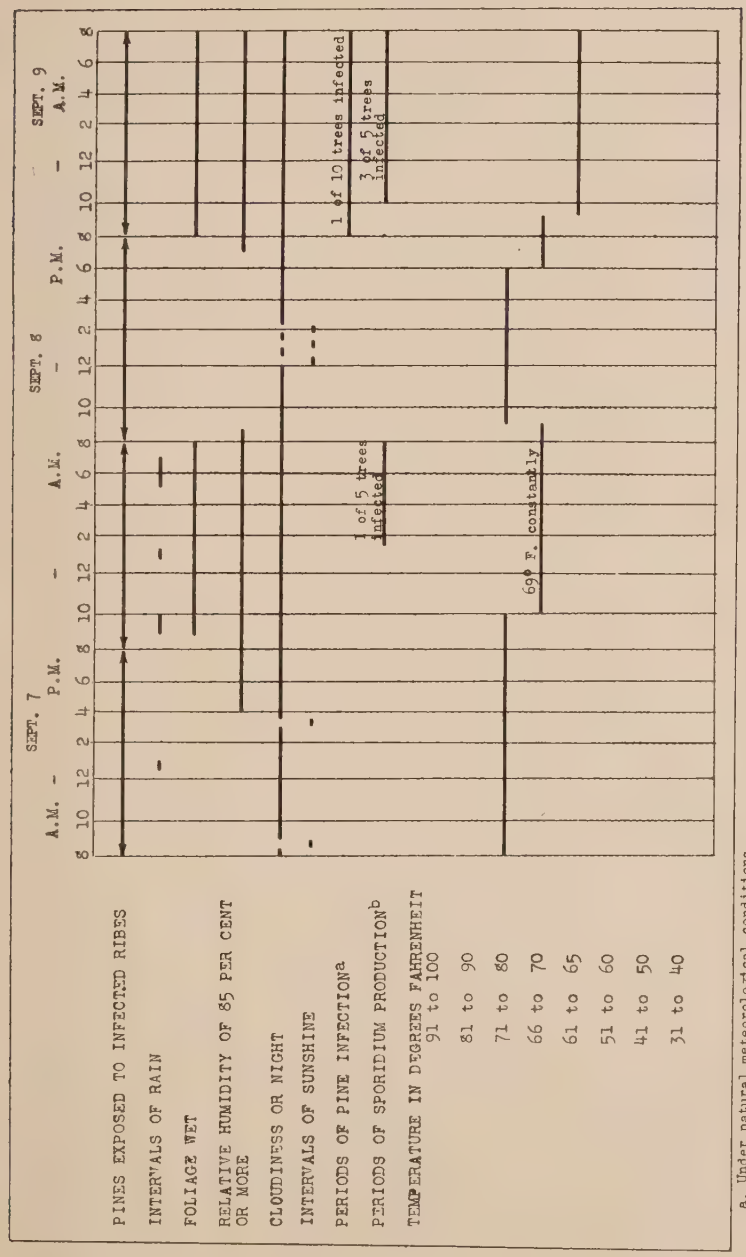
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 29. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1936.



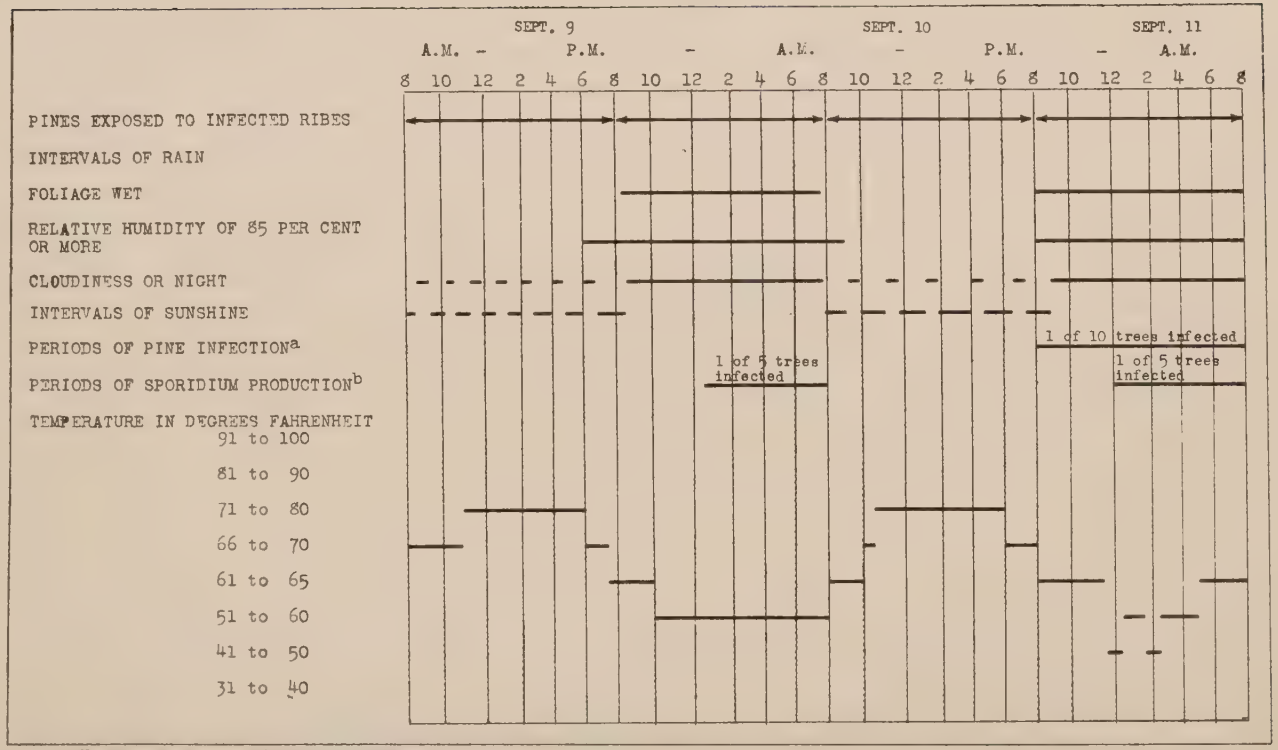
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 30. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1936.



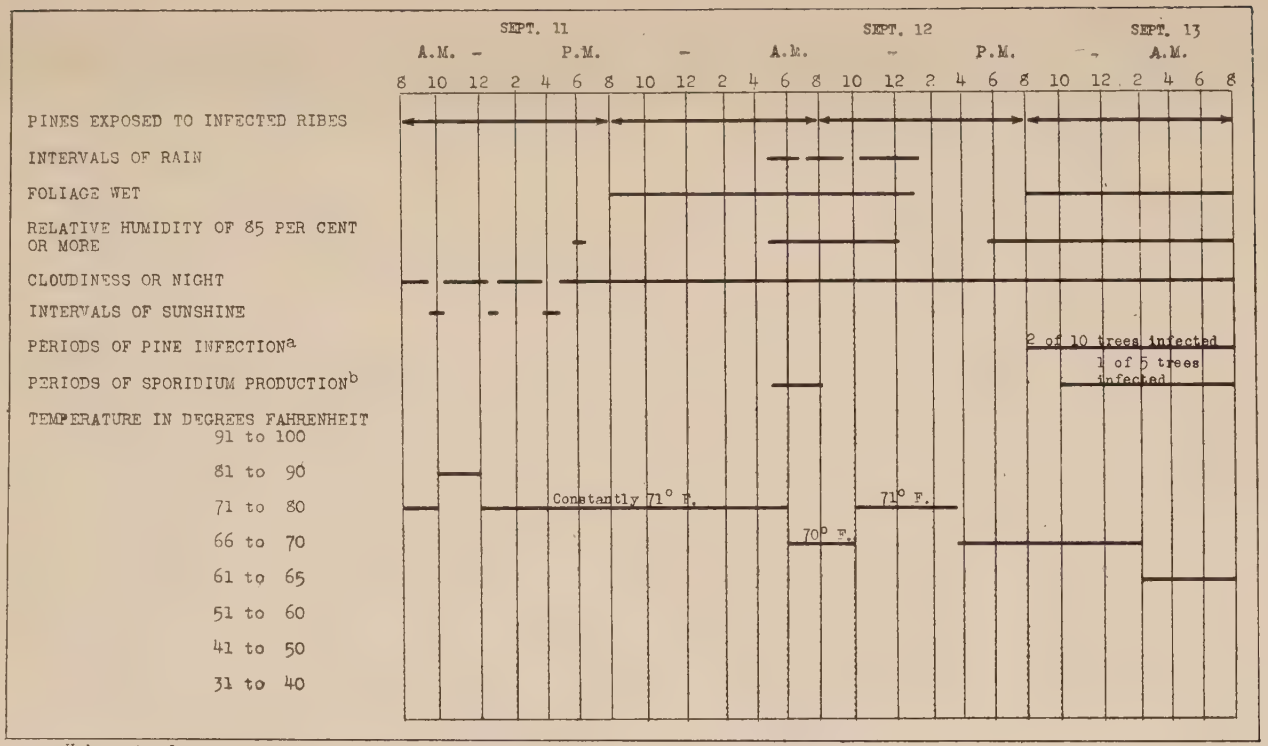
a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 31. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1936.



a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 32. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1936.



a. Under natural meteorological conditions.
b. Shown by microscopic studies, infection of damp-chamber trees and trees exposed to natural conditions.

Fig. 33. Data relative to the infection of young white pine trees exposed to telium-bearing ribes for 12-hour periods in 1936.

subjected to a relative humidity as low as 58 per cent; as much as 68 per cent of the viable sporidia sticking to telial columns on living ribes leaves in the morning were found to remain viable throughout a clear, hot, summer day. When telium-bearing ribes leaves were turned so as to expose the telia to direct sunlight, as much as 5 per cent of the sporidia present in the morning were still viable at the end of 7 hours. These data are of assistance in interpreting the results of pine infection under natural conditions.

PINE INFECTION

Time necessary for infection.—After sporidia of *Cronartium ribicola* contact the foliage of susceptible 5-needled pines, favorable atmospheric conditions must continue for a number of hours before the fungus can become established within the pine needles. This interval of time has been reported as varying from 6 hours (22) to 12.5 hours (21). It also has been suggested that approximately 18 hours of favorable weather is sufficient for sporidia to be produced and disseminated, and to result in some infection of white pine (19).

Two attempts were made to secure more information regarding the time required for needle infection subsequent to inoculation. Two sets of 40 trees each were used at 2 different times, the 2 sets being treated alike. In order to secure a uniform deposition of sporidia on the pines, fresh telium-bearing leaves of *Ribes nigrum* were placed, with the spore-bearing surface of each leaf down, on a coarse wire screen just beneath the ceiling of a specially constructed damp chamber that retained a relative humidity of 100 per cent and a temperature of 63° F. to 65° F. The leaves were moistened with a misty spray of water. The abundance of sporidia and their uniformity of distribution were determined by means of solidified water-agar spore traps located at different places in the damp chamber. When sporidium production and dissemination were satisfactory, 40 potted pines of approximately equal size were placed on the floor of the damp chamber. At the end of 1 hour it was ascertained that an abundance of sporidia had been produced and uniformly distributed at the level of the pine foliage. The ribes leaves were removed at once and also 4 of the potted pines. Three hours later 4 more pines were removed and at the end of each 4 hours thereafter, 4 pines were taken out of the chamber until the last 4 were removed at the end of 36 hours. Upon removal from the damp chamber, each tree was thoroughly washed under a strong jet of water, after which the excess water was shaken from the tree. After this treatment, the trees were placed in a very dry room at 70° F. for a minimum of 24 hours and later subjected to a day of sunshine before being planted permanently in a plantation. That is, the treatment of each pine was such that presumably infection could occur only while it was in the damp chamber. Under these conditions, the minimum time required for pine infection

following inoculation was 8 hours (Table 2). Adding to this the minimum of 3.5 hours required for sporidium production, a total of 11.5 hours is indicated as the minimum time for pine infection. The presence of infection in the trees was based wholly on the development of bark cankers. Although needle infection was demonstrated to occur within a minimum of 8 hours after inoculation in a controlled environment, more trees developed cankers when they were kept in the damp chamber for 16 hours and longer. Requirements for infection under natural conditions agreed in general with those under controlled conditions. The 12-hour exposure period used throughout most of this work was sufficient to permit pine infection under natural meteorological conditions (Figs. 5 to 11, 16, 23, 24), but more pronounced infection resulted during longer periods favorable to pine infection (Figs. 17, 21, 25, 29).

TABLE 2.—TIME REQUIRED, FOLLOWING INOCULATION OF WHITE PINE BY SPORIDIA OF CRONARTIUM RIBICOLA, FOR INFECTION TO BECOME ESTABLISHED AT TEMPERATURES OF 63°F. TO 65°F.

Time required for infection in hours	No. of trees exposed	No. of trees infected	No. of infections
1	8	0	0
4	8	0	0
8	8	1	1
12	8	1	1
16	8	2	2
20	8	2	3
24	8	4	4
28	8	2	4
32	8	1	1
36	8	3	8

Figures 5 to 11 disclose that most of the infections were upon those pines exposed to the blister rust at night. This may have been due in part to the fact that in the experimental areas, free moisture was usually present on ribes and pine foliage between 8 P.M. and 8 A.M., and the temperatures were commonly near optimum for sporidium germination.

Temperature influence.—Temperature has been shown to affect sporidium production and germination, consequently it is an important factor governing the infection of 5-needled pines by *Cronartium ribicola*. From 1930 to 1936 inclusive, most of the infections under natural conditions and under the conditions of the damp cham-

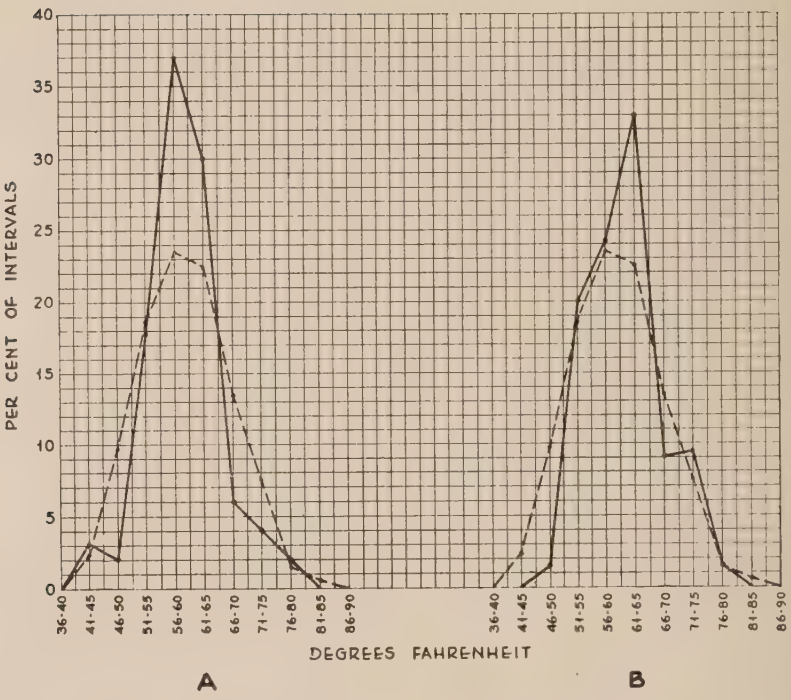


Fig. 34. Broken-line curves represent 298 intervals of rain, fog, and dew for certain months in 1930 to 1936, inclusive, arranged according to the temperatures averaged over the 12-hour periods concerned. A. Solid curve gives the distribution of the intervals according to average temperatures at which the damp-chamber plants became infected. B. Solid curve gives the distribution according to average temperatures at which natural infection of white pine occurred.

ber took place during the following months: July and August, 1930; August and September, 1931, 1933, 1936; August, 1932; and September, 1935. In these months there was a total of two hundred and ninety-eight 12-hour periods with moisture in the form of rain, fog, or dew, during which there was an abundant supply of viable teliospores on the ribes in the garden. These periods were distributed according to temperatures shown in figure 34. Pine infection under natural meteorological conditions developed during 53 of these periods, the majority of which had average temperatures ranging between 51°F. and 66°F. The damp-chamber trees, used to demonstrate sporidium production, developed infections during 74 of the 298 periods, the majority of which had temperatures within the above range. The contours of the infection curves in figure 34 are no doubt influenced to some degree by the relative order in which the intervals of rain, fog, and dew occurred. This is of some importance in interpreting, from the curves, the effects of temperature upon pine infection. However, the cardinal temperatures indicated for infection are approximately the same as those previously determined for sporidium production and germination (5), and the apices of the infection curves are higher and sharper than those of the curve showing the distribution of the nights with moisture available for the establishment of the rust fungus. Pronounced infection took place when the temperatures for a 12-hour period averaged below 70°F., usually within the range of 50°F. to 68°F. and rarely took place when the temperature averaged above 70°F.

The effects of various temperatures upon needle infection are illustrated also by the diagrams of daily records of infection, temperature, and moisture (Figs. 5 to 11). Moisture for pine infection was present almost continuously from August 6 to August 12, 1937, and daily microscopic examinations of telial columns showed that they were mature; germination tests under artificial conditions disclosed that they were composed largely of viable teliospores. Only a relatively few of these telial columns, however, produced sporidia and then only in small numbers during those 24-hour periods. No pine infection took place. The lack of pine infection during that week of rainy weather appeared to result from the failure of sporidium production brought about by the high temperature. On the night of August 13, the temperature dropped to 56°F. for a brief interval and sporidium production increased noticeably although no pine infection resulted. Weather data for some of the infection periods are shown in more detail in figures 12 to 33. The period of August 12 to August 14, 1933 (Fig. 15) illustrates a period shorter but otherwise similar to that of August 6 to 12, 1937. During the night of August 12, 1933, with a temperature of 56°F. to 60°F., 1 of 2 damp-chamber trees became infected; the night of August 13 with a temperature of 60°F. to 65°F. both of the damp-chamber trees developed blister rust. With showers during the intervening 12-hour daylight period, there was

ample moisture for infection but none occurred. The temperature reached 77°F. for 1 hour but ranged slightly below 70°F. for the remainder of the 12-hour period, which suggests that the constant, high temperature was the factor which adversely affected the production of sporidia. In contrast with that period is the period of August 21 and 22 (Fig. 17) of the same year. All of the trees exposed during the night of August 21 became infected; of the 5 trees exposed during the day of August 22, 2 developed cankers; and of the 5 trees exposed during the night of August 22, 4 became infected. In this instance the temperature of the daytime period never exceeded 66°F. and most of the time was 65°F. or lower; showers provided moisture during the day. Thus with the temperature within the optimum range, infection took place throughout the 3 consecutive 12-hour periods.

The effect of temperatures constantly near the maximum for pine infection is illustrated by the day periods of August 24 and September 3, 1933, day of September 12, day and night of August 15, and nights of September 7 and 11, 1936 (Figs. 18, 21, 26, 31, 33). During the 12-hour day period of August 24, 1933, rain was continuous and the temperature held constantly at 68°F. and 69°F.; no infection took place although infection did occur on 4 of 5 trees the preceding night when the temperature was 65°F. to 66°F. from 8 P.M. to 2 A.M. and then slowly rose to 68°F. During the daylight period of September 3 no infection occurred; misty rain was continuous and the temperature again was constantly at 68°F. and 69°F. On the nights of September 2 and 3 the temperature was at or below 65°F. and during each of the two 12-hour periods, heavy infection developed on 3 of 5 trees. In 1936, the night temperatures of August 14 and 15 were 69°F. and 71°F., respectively. No natural infection took place although free water was constantly present and microscopic examinations of the telia disclosed that sporidia were produced. Moreover the presence of infection upon the damp-chamber plants exposed during the night of August 14 proved that sporidia had been disseminated to the pines. Similar weather conditions prevailed September 7, 11, and 12 with the like results. That the high temperatures rather than the evenness of temperature adversely affected pine infection is demonstrated by the contrasting results obtained the nights of September 3, 1933, September 8, 1935, and September 2, 1936 (Figs. 21, 25, 29) when the temperatures were relatively nonfluctuating but well below 68°F.; quite heavy natural pine infection took place each night. The infection data suggest that although pine infection may take place when a fluctuating temperature ranges between 65°F. or below to as high as 70°F. or slightly above, temperatures constantly within a range of 68°F. and 69°F. or above may inhibit pine infection even though other factors are particularly favorable.

Few data on minimum temperatures that permit pine infection were secured. Light infection of *Pinus strobus* took place on potted

pines in a damp chamber at a temperature of approximately 32°F. Of 20 trees used, 1 tree became infected within 36 hours and 2 trees in 72 hours. Among 12 inoculated trees subjected to a constant temperature range of 34°F. to 36°F., 1 tree became infected within 24 hours. These data are of value only to show that infection of *P. strobus* may take place at approximately the freezing temperature of water when other factors are favorable. In nature, infection of pine at these low temperatures probably rarely if ever occurs.

Relative importance of rain, fog, and dew.—When telia were present on ribes in the experimental areas, moisture was available for natural pine infection chiefly as rain, fog, and dew.

While rain is falling and for a brief time afterward, water may occur as a continuous film on the ribes and pine foliage; during fog and dew it is more apt to occur in the form of minute drops on the leaf surfaces, although in heavy fog the drops of water sometimes coalesce to form a film. The length of time that this free water is available for the germination of fungus spores varies with the different atmospheric conditions associated with the moisture periods. Air movements are commonly more rapid during rain than during fog and dew, and are more rapid during fog than during dew, so that the 3 different atmospheric conditions probably have unlike effects upon the dissemination of the wind-borne sporidia and upon their potential infecting powers. For this reason a study was made of the effects of rain, fog, and dew on the infection of eastern white pine by the blister-rust fungus.

In order to compare the effects of the 3 different moisture conditions on pine infection for the years 1930 to 1933 and 1935 to 1936 inclusive, only nights of rain, fog, and dew combined with cardinal temperatures for pine infection are considered. The number of telium-bearing ribes leaves in the garden varied somewhat during the several summer seasons. However, nights of rain, fog, and dew were interspersed sufficiently so as to eliminate the somewhat irregular quantity of inoculum as a serious factor favoring any particular moisture form. In the test area near Warrensburg, nights with rain, fog, and dew were frequent; near Syracuse, rains and dew were frequent but fog occurred only occasionally.

Blister-rust cankers developed on pines exposed in the ribes garden during 21 nights of rain, 18 nights of fog, and 10 nights of dew (Table 3), that is, infection developed 1 night during approximately every 5 nights with rain, 7.5 nights with fog, and 12.5 nights with dew. On this basis rain and fog proved to be most important to pine infection. However, the number of infections that developed under each of the 3 moisture conditions was considered to bear more weight in evaluating the relative effects of the 3 moisture conditions. By dividing the number of infections that developed during rain, fog, and dew respectively by the number of times that each moisture form was present, their respective relative importance to pine infection is found to be

TABLE 3.—A RECORD OF WHITE PINE INFECTION BY THE BLISTER-RUST FUNGUS UNDER PREVAILING WEATHER CONDITIONS DURING NIGHTS WITH RAIN, FOG, OR DEW

Location	Year	Moisture Condition														
		Rain					Fog					Dew				
		No. of nights with rain	No. of nights on which infection occurred	No. of trees infected	Per cent of trees infected	No. of infections	No. of nights with fog	No. of nights on which infection occurred	No. of trees infected	Per cent of trees infected	No. of infections	No. of nights with dew	No. of nights on which infection occurred	No. of trees infected	Per cent of trees infected	No. of infections
Warrensburg, N. Y.	1930	24	2	2	1.42	2	26	2	3	2.30	4	15	1	1	1.33	1
	1931	23	7	14	12.17	27	38	9	17	8.94	25	17	1	1	1.17	1
	1932	14	1	1	1.43	1	39	2	3	1.54	3	13	0	0	0.00	0
	1933	18	4	15	16.67	55	30	4	7	4.67	11	19	1	1	1.05	2
Syracuse, N. Y.	1935	17	2	9	5.29	19	0	0	0	0.00	0	46	4	7	1.52	11
	1936	10	5	21	21.00	56	2	1	2	20.00	3	17	3	4	2.35	5
Total		106	21	62		160	135	18	32		46	127	10	14		20
Average					9.67					7.49					1.23	

10:2:1. On this basis rain provided, by far, the most suitable moisture condition for the natural infection of *P. strobus*.

Infection took place on damp-chamber plants on some nights when natural infection failed (Figs. 5 to 11). Less than one-half as many pines were used for damp-chamber studies as were employed under natural meteorological conditions; consequently, for the sporidia the total target of pine needles was proportionately less. In spite of that, of the 368 nights that pines were exposed (Table 4), infection of the damp-chamber plants occurred during 78 nights, as compared with 49 nights for the pines under natural conditions. That is, sporidium production and dissemination took place during 29 nights when all the natural factors were not conducive to pine infection. It may be assumed that under the natural outdoor conditions during these 29 nights, the factors favoring sporidium production were also suitable for needle infection but the favorable conditions failed to persist sufficiently long, subsequent to inoculation, for the establishment of the young hyphae in the pine needles. This might be the situation if sporidia were not produced in sufficient abundance to insure their deposition upon pine foliage until the latter part of a 12-hour night period. The adverse effects of high temperature and low relative humidity of a following daylight period would then inhibit infection under natural conditions but not in the environment of the damp chamber. The production of abundant sporidia during 29 nights when natural infection did not take place was important, since this reduced the number of viable teliospores on the ribes leaves and lowered the sporidium production that might have occurred when meteorological factors did favor pine infection. Considering only the infections on the damp-chamber plants and computing in the same way as for the infection under natural meteorological conditions, the relative importance of rain, fog, and dew, respectively, to sporidium production was 10:7:2. On this basis fog was nearly as important as rain in stimulating sporidium production. In view of the fact that, when compared with rain, fog resulted in relatively high sporidium production but relatively low pine infection, this moisture condition may be an important factor in reducing the potential pine-infecting power of the blister-rust fungus when fog and optimum temperatures occur quite regularly during summer and early autumn and when rain periods are widely separated.

Importance of weather preceding and following favorable infection periods.—It has been indicated that at least 11.5 hours of favorable meteorological conditions are essential for pine infection and longer periods favor heavier infection. Therefore, since most of the pine infection took place at night, it may be assumed that the character of the daylight periods that preceded and followed the favorable night periods greatly influenced the chance for and amount of infection at night. This seems obvious because a clear day with low humidity preceding a favorable night period might delay sporidium

TABLE 4.—A RECORD OF INFECTION ON WHITE PINE TREES WHICH WERE EXPOSED TO NATURAL INOCULATION BY THE BLISTER-RUST FUNGUS DURING NIGHTS OF RAIN, FOG, OR DEW AND THEN KEPT FOR 36 HOURS IN A DAMP CHAMBER WITH TEMPERATURE AND MOISTURE FACTORS FAVORABLE FOR PINE INFECTION

Location	Year	Moisture Condition														
		Rain					Fog					Dew				
		No. of nights with rain	No. of nights on which infection occurred	No. of trees infected	Per cent of trees infected	No. of infections	No. of nights with fog	No. of nights on which infection occurred	No. of trees infected	Per cent of trees infected	No. of infections	No. of nights with dew	No. of nights on which infection occurred	No. of trees infected	Per cent of trees infected	No. of infections
Warrensburg, N. Y.	1930	24	6	8	16.67	22	26	11	15	28.85	24	15	0	0	0.00	0
	1931	23	4	4	8.69	17	38	12	13	17.11	25	17	2	2	5.88	3
	1932	14	3	3	10.71	4	39	7	10	12.82	16	13	0	0	0.00	0
	1933	18	5	6	16.67	15	30	9	9	15.00	19	19	1	1	2.63	2
Syracuse, N. Y.	1935	17	2	2	2.35	4	0	0	0	.....	0	46	2	2	0.87	2
	1936	10	6	15	30.00	48	2	1	1	5.00	7	17	7	14	16.47	17
Total		106	26	38	.....	110	135	40	48	.....	91	127	12	19	.....	24
Average		.....	.....	.....	14 18	.....	.....	.....	.....	15 75	.....	.....	.....	.....	4.31	.....

production several hours, which is sufficient to prevent or at least reduce pine infection (Figs. 12, 19, 24, 28). A similar day following a favorable night would surely destroy the viability of most of the newly cast sporidia as well as prevent the establishment in pine needles of many young germ tubes from germinating sporidia (Figs. 14, 30, 32). Favorable weather for sporidium production and pine infection during daylight periods would tend to have the reverse effects (Figs. 17, 18, 21, 25, 29).

Table 5 lists the number of 12-hour day and night periods with rain, fog, and dew, which were present in the course of the work from 1930 to 1936 while the temperature ranged within 48°F. to 70°F., inclusive. Infection occurred once in every 5 periods of rain, 6 periods of fog, and 11 periods of dew. The one hundred and thirty-eight 12-hour periods with rain averaged 1.0 cankers per period; the 127 periods with fog averaged 0.4 cankers per period; and the 119 periods with dew averaged 0.2 cankers per period.

With other factors favorable for pine infection and without regard to the form in which moisture occurred, the amount of infection during a 12-hour period was influenced decidedly by the weather conditions of the 12-hour periods immediately preceding and following. When 12-hour periods with conditions favorable for pine infection were followed by rain, infection occurred once in every 5 periods and averaged 1.26 cankers per possible period; when followed by clouds, once in every 8 periods averaging 0.37 cankers per period; when followed by sun, once in every 17 periods and averaged 0.49 cankers per period; no cankers are recorded when followed by dew and only 1 canker when followed by fog. Hence intervals of rain following 12-hour periods favorable to pine infection resulted in a greater amount of infection than did intervals of either clouds or sunshine. Probably the inhibiting effects of a day of sunshine following favorable infection weather is greater than indicated here, inasmuch as 31 of the total number of infections took place during 1 of 6 periods followed by sunshine (Table 5).

When 12-hour periods with conditions favorable for pine infection were preceded by rain, infection occurred once in every 4 periods and averaged 1.12 cankers per period; when preceded by clouds, once in every 9 periods with 0.52 cankers per period; and when preceded by sun, once in every 16 periods averaging 0.16 cankers per period. There were insufficient periods with dew and fog preceding infection periods to be indicative.

These data indicate that sunshine preceding or following 12-hour periods favorable for pine infection appreciably reduces the amount of infection that might otherwise occur if the preceding or following periods are accompanied by rain or cloudiness. The data also emphasize the importance of prolonged rain periods for the intensification of the rust upon white pine and clearly show that more infection

TABLE 5.—INFECTION OF WHITE PINE BY THE BLISTER-RUST FUNGUS DURING 12-HOUR PERIODS OF VARIOUS WEATHER CONDITIONS

	Rain Periods					Fog Periods					Dew Periods				
	No. of infections	No. of 12-hour periods in which infection occurred	No. of 12-hour periods of rain	Moisture period		No. of infections	No. of 12-hour periods in which infection occurred	No. of 12-hour periods of fog	Moisture period		No. of infections	No. of 12-hour periods in which infection occurred	No. of 12-hour periods of dew	Moisture period	
				Preceded by	Followed by				Preceded by	Followed by				Preceded by	Followed by
	54	9	27	rain	rain	6	1	8	rain	rain	0	0	1	rain	rain
	22	5	26	rain	clouds	18	9	24	rain	clouds	4	3	8	rain	clouds
	33	3	4	rain	sun	0	0	6	rain	sun	0	0	6	rain	sun
	1	1	4	rain	fog	0	0	0	rain	fog	0	0	0	rain	fog
	0	5	4	rain	dew										
Total....	110	23	65	.....	.....	24	10	38	.....	.....	4	3	15	.....	.....
	52	5	23	clouds	rain	5	2	6	clouds	rain	5	1	18	clouds	rain
	0	0	17	clouds	clouds	11	5	24	clouds	clouds	8	4	40	clouds	clouds
	0	0	1	clouds	sun	0	0	21	clouds	sun	4	1	15	clouds	sun
						0	0	0	clouds	fog	0	0	0	clouds	fog
Total....	52	5	41	.....	.....	16	7	51	.....	.....	17	6	73	.....	.....
	0	0	7	sun	rain	8	2	7	sun	rain	1	1	8	sun	rain
	0	0	5	sun	clouds	0	0	15	sun	clouds	0	0	11	sun	clouds
	0	0	1	sun	sun	1	1	16	sun	sun	3	1	12	sun	sun
						0	0	0	.....	fog	0	0	0	sun	fog
Total....	0	0	13	.....	.....	9	3	38	.....	.....	4	2	31	.....	.....
	0	0	3	fog	rain	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	0	0	1	fog	sun	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	0	0	2	fog	fog	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	0	0	1	fog	dew	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Total....	0	0	7	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	15	1	8	dew	rain	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	0	0	1	dew	clouds	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	0	0	2	dew	fog	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	0	0	1	dew	dew	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Total....	15	1	12	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

is likely to take place when moisture is supplied in the form of rain than in the form of fog or dew.

There is one important factor that influences pine infection under all conditions but is not brought out by the data presented, namely, the age and condition of the telia during periods of weather conducive to pine infection. It has been stated previously that, although some new telial columns may develop throughout a summer season, the bulk of the telia are produced in crops within relatively short periods, once to several times during a single season. When these telia are approximately 4 to 9 days old, the teliospores appear to be quite sensitive to certain moisture and temperature combinations and produce sporidia more abundantly than at any other time (5). Consequently, the occurrence of suitable weather at such times is more likely to result in heavy pine infection than when telial crops are younger or appreciably older. This may explain in part why much more pine infection occurs in some seasons than others even though the seasons may have approximately the same amount of rainfall and a similar number of hours of high relative humidity.

Pine infection as related to seasons.—Each year 85, 90, or 100 trees of *Pinus strobus* were planted beside bushes of *Ribes nigrum* in the early spring and left until the bushes were completely defoliated in the late autumn, after which the pines were replanted in a permanent site. Each season the exposed pines occupied the same positions in respect to the ribes bushes. The data that are recorded in table 6 were taken only during the time that telia were actually present upon the ribes. Although there were apparently no pronounced meteorological differences between the seasons yet in 1935 and 1936 a relatively large amount of infection developed in comparison with the other 4 years. In 1935 and 1936, 2 of the periods of weather favorable to pine infection coincided with the presence of newly developed crops of telia; consequently, sporidia were produced promptly and abundantly and considerable pine infection followed. In 1932, both periods of favorable weather came at a time when telia were not abundant and those that were present were old and composed in part of germinated teliospores. In 1933, one period of favorable weather came as a telial crop was developing and sporidia were produced in abundance. Consequently, pine infection was greater than in 1932. The low amount of infection in 1937 was due in all probability to the high average temperature for the season, which is reflected in the unfavorably high temperatures for the extended periods when moisture was available for infection. In 1938, no extended periods of favorable weather occurred during the time that new telia were abundant on the ribes. Thus the reason for the pronounced differences in pine infection for the years 1932 to 1938 is not disclosed by the weather data alone but is made known only through a daily study of the rust on ribes in relation to the daily weather.

TABLE 6.—CERTAIN COMPARABLE WEATHER DATA AND PINE INFECTION RECORDS BY SEASONS

Season of infection	Consecutive days of exposure to telium-bearing ribes	No. of days with sunshine for 1 hour or less	No. of 12-hour periods with more than a trace of rain	Periods with relative humidity of 85 per cent or more for at least 24 hours	Av. temperature for periods in column 5 in degrees Fahrenheit	Av. temperature for infection season in degrees Fahrenheit	No. trees exposed	No. surviving trees	Average needle-inches per tree	No. of infections	No. of infections per 1000 needle-inches on surviving trees	Theoretical No. of infections per 1000 needle-inches for a 50-day season
1932	68	8	28	2	51 67	65.1	90	77	1279	50	0.51	0.38
1933	75	9	31	3	64 67 60	66.1	100	98	2723	291	1.09	0.73
1935	79	18	42	3	61 60 51	67.4	85	77	1137	257	2.93	1.85
1936	70	9	22	2	58 68	67.4	85	81	1132	289	3.15	2.25
1937	74	13	37	.5	71 74 71 72 63	70.2	100	95	2219	130	0.62	0.42
1938	59	3	20	0	.....	72.7	100	68	2211	71	0.47	0.40

Pine infection does not depend entirely upon suitable weather conditions, a fact recognized by Pennington in his study of weather relationships to infection of western white pine (14). For pine infection to take place, favorable weather must occur when the fungus is in a stage of development that permits the rapid and plentiful formation of sporidia. Air movements must be suitable to facilitate the dissemination of the sporidia to the pine needles after which specific atmospheric conditions are required for a sufficient duration of time to permit the germination of sporidia and the establishment of young germ tubes in the interior of pine needles. The pine needles must then remain alive and be retained for almost a year (8) in order to allow the young mycelium to reach the bark. Thus pine infection hinges upon a combination of definite conditions and consequently heavy pine infection is more or less sporadic. This is exemplified by figures 5 to 11, which record infection for each year of the study, and by table 6, which compares infection by seasons. Thus it appears doubtful that seasonal weather data alone can be used as a reliable basis for determining whether a particular season may have resulted in a large amount of pine infection by *Cronartium ribicola*.

DISCUSSION AND SUMMARY

A study was made of the relation of certain meteorological factors to the natural and artificial infection of eastern white pine by the blister-rust fungus in northern and central New York.

The particular weather factors that received most attention were temperature, relative humidity, rain, fog, dew, and sunshine. These factors may vary markedly between localized areas not far removed from one another. Consequently, within forest and reforestation areas of large size, there may be localized sites that are more favorably disposed than others toward pine infection. This fact suggests that the same control measures applied over an area as large as New England or even New York may meet with very different results in different localities, and further suggests that control measures need to be more intensive in sections where localized weather conditions are especially favorable to rust spread.

Ribes nigrum was used exclusively as a source of sporidia in this study because of its pronounced susceptibility to *Cronartium ribicola* and the fact that the fungus produces teliospores and sporidia in abundance on this host. Moreover, *Ribes nigrum* has been an important factor in the intensification of the blister-rust fungus in New England and New York. It is logical to assume that when *Cronartium ribicola* grows upon native wild ribes and upon susceptible cultivated species other than *R. nigrum* the production of teliospores and sporidia, if teliospores are produced, will be influenced in the same way by similar weather conditions as it will when the fungus grows on *R. nigrum*. It is known, however, that the blister-rust fungus

varies in its ability to produce urediospores and teliospores on different ribes, and in certain ribes it is able to grow in the leaf tissue only a short time after infection is established (1, 4, 9, 12, 16, 18). There is need of an intensive study of the rust on our native ribes in the East, particularly in respect to its relative pine-infecting powers. Snell (16) has recently indicated that the cultivated red currant may not be a serious agent for the infection of white pine as compared with other ribes.

Teliospores were produced in distinct crops once to several times during each season of the study. By employing certain methods, a fair quantity of telial columns with viable teliospores were kept on the ribes throughout each season so that the effects of the prevailing weather upon pine infection could be studied daily. The production of telial crops appeared to be associated with leaf maturity, leaf condition, and seasonal changes. Moshkov (13) has indicated that teliospore production on *Ribes nigrum* may be associated with length of daylight periods, 13-, 14-, and 15-hour days being best for teliospore development in the region of Leningrad. In the experimental areas in New York, the hours of daylight during the summer and autumn days were within this range so that day length probably had no significant effect upon teliospore production. When the telial crops were 96 to 216 hours old, the teliospores responded most effectively to weather favorable for sporidium production and consequently for pine infection. Thus, each season, pronounced pine infection was restricted to relatively few periods when favorable weather happened to coincide with suitable stages in the development of the rust on ribes. Throughout the years of this study most of the heavy infection periods occurred during the latter part of August, a few came in early September, and one in July.

Teliospores became mature when they were approximately 24 hours old. Thus during the several days that were necessary for the individual telial columns to attain their maximum length, the maturity of the teliospores was progressive from the tip of the columns toward the base. Hence, in the Adirondack experimental area where cool nights with fog were usual during the summer months, some of the outermost viable teliospores in the columns germinated nightly. This was determined by means of spore traps, microscopic examination of the columns each morning, and to some extent by infections on the damp-chamber trees. Thus, mature telial columns were composed in part of exhausted teliospores, and their potential pine-infecting power was reduced accordingly.

The minimum time required for pine infection under optimum moisture and temperature conditions was found to be 11.5 hours, but the amount of infection was greater after 19.5 hours. Thus, although infection may occur during a day or night of favorable weather, extended periods of weather conducive to pine infection will result in more cankers when other factors are favorable.

Throughout the work most of the pine infection occurred at night. Apparently this resulted largely because at night, almost without exception, free moisture was present either as dew, fog, or rain, and the temperature was commonly within the optimum range. Moreover, when rain caused the teliospores to produce sporidia during the daylight hours, the moisture and temperature range of the night that followed were almost always favorable for continued sporidium production and pine infection.

The optimum temperature range for pine infection was found to be approximately 50° F. to 65° F. However, some infection did occur during periods when the temperature reached several degrees above 70° F., but only if the temperature was fluctuating between the higher and lower levels. A constant temperature level of 68° F. to 69° F. was sufficient to inhibit pine infection even though other factors were most favorable. A few sporidia, however, were produced at that temperature level.

In the experimental areas, the important sources of free moisture for sporidium production and pine infection were rain, fog, and dew. The respective order of importance to pine infection was 10:2:1; to sporidium production, 10:7:2. Rain was therefore the most important moisture source for the successful infection of eastern white pine. Fog was almost as effective as rain in stimulating the production of sporidia but only about one-fifth as effective as rain in bringing about pine infection During fog, pine infection resulted during less than half of the 12-hour periods in which sporidia were known to have been formed; consequently, fog was of marked importance to the reduction of the number of sporidia that might otherwise have been available for pine infection. The fact that pine infection did take place during approximately one-half of the fog periods should not be overlooked. Certainly, where fog occurs regularly at night throughout a summer season it will not only induce sporidium production but, with other factors favorable, pine infection will take place, and over a period of years may result in building up infection to the point of severe damage. In fact, within the range of native 5-needled pines it would be possible for fog to be the one source of moisture responsible for heavy pine infection in areas where rains do not occur commonly at the time when telia are abundant.

Dew was of more importance to the exhaustion of teliospores without pine infection than was disclosed by the infections on the damp-chamber plants. Microscopic examinations of telial columns each morning showed that during nights with dew when temperatures were optimum germination of teliospores occurred. This was often true for nights of fog when the damp-chamber plants failed to demonstrate the presence of sporidia.

Although the periods of precipitation were most conducive to pine infection, the character of the 12-hour periods immediately preceding and following periods of rainfall had a definite effect upon the

amount of pine infection. Days of sunshine and high temperature prior to a night of rain tended to delay the production of sporidia so that often there was not sufficient time for pine infection to be accomplished, particularly if the following day was warm and sunny. Cloudiness coupled with relatively low temperatures caused less delay in sporidium production so that some infection commonly took place during nights of rain following cloudy daylight periods.

Every summer most of the pine infection that took place occurred during 1 or 2 relative brief periods of cool, wet weather that happened to coincide with an abundant supply of freshly produced teliospores. This fact indicates that seasonal weather data alone are not a good key to seasonal pine infection except when extremes of temperature and moisture mark the season.

This study has not dealt with weather relationships and the establishment and intensification of the rust upon ribes or with the relative infecting power of the rust incubated on the various native ribes of the Northeast. Preliminary studies indicate differences in the effects of the rust when it grows on certain different species of ribes. Knowledge of the relative infecting power of the rust from the various native ribes in the eastern United States is of importance to the control program and studies are needed to supply such information.

Some control of blister rust may be exercised silviculturally by avoiding the planting of eastern white pine on sites that are unusually favorable, climatically, for pine infection. Plantations established on sites where cool, damp nights are the rule, or established in climatic zones where extended periods of cool rains occur several times during the average summer, may need especially frequent eradication of native ribes with wider protective borders in order to provide maximum protection from the rust. During occasional years the weather is extremely favorable for pine infection, as in 1927, and the eradication of ribes must be frequent and thorough enough on both favorable and unfavorable sites to secure adequate protection. Modifications in eradication practices can probably be more safely made on various sites when knowledge of the relative infecting-power of the rust from the different native ribes species under various weather conditions becomes available.

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